A REVISION OF THE DEVONIAN (EMSIAN-EIFELIAN) TRILOBITA FROM THE BOKKEVELD GROUP OF SOUTH AFRICA

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(With 120 figures)

[*MS accepted 20 January 1982*]

ABSTRACT

The Bokkeveld trilobite fauna is revised and shown to comprise the following species: *Ormistoniella malaca* (Lake), *Malimanaspis? dereimsi* (Kozlowski), *Burmeisteria herscheli* (Murchison), *B. notica* (Clarke), *B. fontinalis* (Reed), *Francovichia clarkei* (Ulrich), *Gamonedaspis boehmi* (Knod), *Oosthuizenella ocellus* (Lake), *Pennaia pupillus* (Lake), *Metacryphaeus caffer* (Salter), *M. venustus* Wolfart, *M.* cf. *koukharskii* (Baldis & Longobucco), *Typhloniscus baini* Salter, *Phacopina hexensis* (Reed), *P. lakei* (Reed), *P.* cf. *padilla* Eldredge & Branisa, *Phacopina?* sp. nov?, *Renniella rossouwi* gen. et sp. nov., *Bainella africana* (Salter), *B. arbuteus* (Lake), *B. cristagalli* (Woodward), *B. gamkaensis* Rennie, *Bainella* sp. nov., *Deltacephalaspis pseudoconvexus* (Reed), and *Kozlowskiaspis ceres* (Schwarz). The affinities of the fauna are clearly with Bolivia. Three new genera are proposed, the dechenellid *Ormistoniella*, and the calmoniids *Oosthuizenella* and *Renniella*, as well as the new calmoniid subgenus *Metacryphaeus* (*Wolfartaspis*). The only new species is *Renniella rossouwi*. At this stratigraphic level *Digonus* and *Burmeisteria* are inseparable, and the former taxon is herein considered superfluous; it is treated as a junior subjective synonym of *Burmeisteria* s.s. Higher calmoniid taxonomy is unsatisfactory and in need of phylogenetic analysis. The trilobite assemblages from the Gydo, Voorstehoek and Waboomberg Formations are distinct, and form the basis for the recognition of the *Bainella africana*, *Metacryphaeus caffer*, and *M. venustus* Assemblage Zones respectively. Commencement of Bokkeveld sedimentation is related to late Emsian eustatic transgression, an age determination supported by the trilobite faunas, with marine deposition extending well into the Eifelian.

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Ann. S. Afr. Mus. **89** (1), 1982: 1–174, 120 figs.

INTRODUCTION

On 25 May 1836 Sir Roderick Murchison announced to the Geological Society of London the discovery by Sir John Herschel of trilobites '. . . in rocks which occur to the north of the Cape of Good Hope', associated with other fossils which, together, '. . . were found in abundance in the Cedar Bergen, according to Captain Alexander 150 English miles north of Cape Town and 2 000 feet above the sea, in an ash-grey quartzose sandstone' (Sandberger 1853: 581). The trilobites were subsequently identified by Murchison (1839) as *Homalonotus herscheli* sp. nov. and *Calymene blumenbachi* Brongniart, the latter a misidentification of what is now *Oosthuizenella ocellus* (Lake) (see p. 65). It was Salter (1856), however, who was the first to describe a major collection of invertebrate fossils from the Bokkeveld succession, including the trilobites *Homalonotus herscheli* Murchison, *Phacops* (*Cryphaeus*) *africanus* sp. nov., *Phacops caffer* sp. nov., and *Typhloniscus baini* gen. et sp. nov. Thus, this work is important in providing the first descriptions of the wholly Malvinokaffric trilobite genera *Bainella*, *Metacryphaeus*, and *Typhloniscus*. In his subsequent monograph of the British trilobites, Salter (1865) created the new subgenus *Burmeisteria* within *Homalonotus*, with *H. herscheli* as the type species.

Woodward (1873) described a highly ornate trilobite with long axial spines from the Cockscomb Mountains in the eastern Cape as *Encrinurus cristagalli* sp. nov., whilst Schenk (1888) mentioned a '*Praetus ricardi*' from the same locality, but without figure or description and hence the name is a *nomen nudum*. In 1897 Frech figured a specimen from the 'Cape Colony' as *Homalonotus perarmatus* sp. nov.

In the first work devoted entirely to a study of the Bokkeveld Trilobita, Philip Lake (1904) recorded the following species: *Phacops pupillus* sp. nov., *P. arbuteus* sp. nov., *P. ocellus* sp. nov., *P. africanus* Salter, *P. cristagalli* (Woodward), *P. (Cryphaeus) caffer* Salter, *Typhloniscus baini* Salter, *Dalmanites lunatus* sp. nov., *Proetus malacus* sp. nov., *Homalonotus herscheli* Murchison, *H. quernus* sp. nov., and *H. colossus* sp. nov., and considered

H. perarmatus Frech a synonym of *H. herscheli*. Soon afterwards Schwarz (1906) further added to the list of Bokkeveld trolibites when describing the material housed in the Albany Museum, Grahamstown, including *Phacops cristagalli* (Woodward), *P. acacia* sp. nov., *P. (Cryphaeus) callitris* sp. nov., *P. (C.) ceres* sp. nov., *P. (C.) gydowi* sp. nov., *Proetus ricardi* Schenk, *Homalonotus herscheli* Murchison, *H. perarmatus* Frech, *H. lex* sp. nov., *H. agrestis* sp. nov., *H. horridus* sp. nov. and *H. hippocampus* sp. nov.

In a discussion of the Bokkeveld fauna, Reed (1907) pointed out that the subgenus *Cryphaeus* could not be applied to trilobites for reasons of priority, and noted that the Bokkeveld phacopids fell into two groups. For *Phacops caffer*, *P. ocellus*, *P. impressus*, *P. callitris*, *P. gydowi*, and *P. ceres* he proposed the name *Metacryphaeus*, while considering *P. africanus*, *P. acacia*, *P. arbuteus*, and *P. cristagalli* to '. . . fall into another group which in many respects resembles that containing *Dalmanites anchiops* Green' (p. 168). For the latter group he proposed the name *Anchiopella*.

In describing *Pennaia africana* sp. nov. from Osplaats in the Hex River valley, Shand (1914) was the first to report the presence of this genus in the Bokkeveld fauna although, as noted by Rennie (1930), the species was generically misidentified. In a discussion of the genus *Homalonotus*, Reed (1918) referred all the South African species to the subgenus *Burmeisteria*.

The most comprehensive discussion of the Bokkeveld Trilobita till now is Reed's (1925*a*) monographic 'Revision of the fauna of the Bokkeveld Beds' in which he described or discussed the following taxa: *Proetus malacus* Lake, *P. hexensis* sp. nov., *Cyphaspis dereimsi* Kozlowski, *Dalmanites* (*Anchiopella*) *africanus* (Salter), *D. (A) cristagalli* (Woodward), *D. (A.) arbuteus* (Lake), *D. (A.) baini* sp. nov., *D. (Corycephalus?) capensis* sp. nov., *D. (Hausmannia) lunatus* Lake, *D. (H.) dunni* sp. nov., *D. (Proboloides) ensifer* sp. nov., *D. (Acastella?) pseudoconvexus* sp. nov., *D. (Cryphaeus) caffer* (Salter), *D. (C.) caffer* var. *albana* var. nov., *D. (C.)* cf. *pentlandi* Salter, *D. (C?)* cf. *rostratus* Kozlowski, *D. (C?) ceres* (Schwarz), *Phacops* (*Calmonia*) *callitris* Schwarz, *P. (C.) impressus* Lake, *P. (C?) lakei* sp. nov., *P. (C?) pupillus* Lake, *Phacops (Pennaia) gydowi* Schwarz, *P. (P.) africanoides* nom. nov. (pro *Pennaia africana* Shand), *P. (Phacopina) hiemalis* sp nov., *Homalonotus* (*Burmeisteria*) *herscheli* Murchison with the varieties *colossus* Lake, *rectisuturalis* var. nov., *fusiformis* var. nov., *grahami* var. nov., *bituberculata* var. nov., *perarmata* Frech, and *sodalis* var. nov., *H. (B.) quernus* Lake, *H. (B?) hippocampus* Schwarz, *H. (Digonus) fontinalis* sp. nov. and *H. (D.) noticus* var. *africana* var. nov. Reed (1925*b*) subsequently proposed the new genus *Eocorycephalus* to include *Dalmanites (Corycephalus?) capensis* Reed from the Bokkeveld sequence.

In reviewing work on the Phacopidae, Reed (1927) contended that *Phacops* (*Cryphaeus*) *caffer* Salter, which he had earlier listed as a species of *Metacryphaeus*, was, in fact, a typical *Asteropyge* and, since the remaining species cited in his original proposal of the genus *Metacryphaeus* could all satisfactorily be included in *Calmonia*, the name should be abandoned. Moreover, he stated that '. . . the type which was chosen for this special group (*Anchiopella*) and exemplified by *Dalmanites anchiops* Green was *Phacops crista-galli* (Woodw.)' (p. 210), while now referring *Phacops gydowi* and *Acaste verneuili* d'Orbigny to the genus *Pennaia*.

Rennie's (1930) revision of the Bokkeveld 'phacopids' was important for its attempt to stabilize nomenclature. Thus he showed that *Metacryphaeus* was a valid taxon whose type species was *Phacops caffer*, that *Eocorycephalus* was a junior subjective synonym of *Synphoria*, and that *Eocorycephalus capensis* (Reed) was founded upon damaged cephala of *Metacryphaeus caffer*. Rennie also transferred all Reed's (1925*a*) Bokkeveld species of *Dalmanites (Anchiopella)* to his new genus *Bainella*, because he erroneously believed (see Cooper 1982) *Dalmanites anchiops* Green to be the type species of *Anchiopella*. In this work Rennie (1930) described and/or figured *Dalmanites (Metacryphaeus) caffer* (Salter), *D. (M?) ceres* (Schwarz), *Acaste (Pennaia) impressus* (Lake), *A. (Calmonia) callitris* (Schwarz), *A. (C.) africana* (Shand), *Bainella bokkeveldensis* sp. nov. *B. gamkaensis* sp. nov., *B. acacia* (Schwarz), *B? africanus* (Salter), and *Typhloniscus baini* Salter.

In 1951 Brink figured and described a large trilobite eye from the Bokkeveld Beds that was identified only as *Phacops* sp. Pillet (1954) discussed the classification of the phacopid trilobites and created the new genus *Paradalmanites* for *Phacops acacia* Schwarz. *Paradalmanites* was correctly included in the synonymy of *Bainella* by Struve (*in* Harrington *et al.* 1959) who also rightfully elevated *Metacryphaeus*, *Calmonia*, and *Pennaia* to generic status.

Although not dealing directly with the Trilobita from the Bokkeveld succession, the works of Wolfart (1968), Braniša & Vaněk (1973), Eldredge & Ormiston (1979), and Eldredge & Braniša (1980) on the Bolivian faunas have a direct bearing on the classification of the Bokkeveld material. Wolfart's (1968) important study showed that *Metacryphaeus caffer* in South America was a catch-all for a number of well-defined species of *Metacryphaeus*, thus pointing to the impressive speciation and adaptive radiation that occurred in the strongly transgressive deposits of the Malvinokaffric Realm. Braniša & Vaněk (1973) created a number of new calmoniid and dalmanitid genera, some of which are now known also to occur in South Africa. Eldredge & Ormiston (1979) reviewed the Malvinokaffric faunas and provided a tentative modern supraspecific revision of the Bokkeveld fauna. Salient features of this review include reference of *Dalmanites dunni* to the genus *Francovichia*, *Proetus malacus* to *Dechenella?*, *Phacopina hiemalis* to *Bainella?*, *Proboloides ensifer* to *Schizostylus* (*Curuyella*), the eye figured by Brink (1951) to the genus *Fenestraspis*, and *Cyphaspis dereimsi* to *Otarion* (*Maurotarion*). The study of Eldredge & Braniša (1980) is of the utmost importance to an understanding of calmoniid taxonomy, again highlighting the complex speciation that occurred in this closed evolutionary pool. These workers provided a revised diagnosis of *Bainella* and created the new subgenus *B. (Belenops)* to include *Bainella* *gamkaensis* Rennie. They also figured a cephalon of *Bainella bokkeveldensis* Rennie, and provided a schematic representation of the auxiliary impression system of a *Pennaia* from Gamkapoort.

As it is now 50 years since the last paper was published dealing specifically with Bokkeveld trilobites, the group is obviously in need of modern revision. This is emphasized by the study of Eldredge & Branišа (1980), which has shown the Malvinokaffric trilobites to be largely endemic. Thus, such European taxa as *Acaste*, *Phacops*, *Dalmanites*, *Homalonotus*, and *Otarion* are not present in the Bokkeveld fauna, but are represented by closely allied or homoeomorphic taxa. The aim of this paper is, therefore, to provide a modern revision of the Bokkeveld fauna on the basis of type and additional material. In this way it is hoped to recognize any zonal succession that may exist and, if possible, to attempt to date the Bokkeveld succession on the basis of the trilobite faunas.

The following abbreviations are used to indicate the repositories of material discussed in the text:

AM	Albany Museum, Grahamstown
BPI	Bernard Price Institute for Palaeontological Research, Johannesburg
BM	British Museum (Natural History), London
KM	Alexander Macgregor Museum, Kimberley
PEM	Port Elizabeth Museum, Port Elizabeth
PRV	Geological Survey, Pretoria
RO	Roy Oosthuizen Collection, Zwartskraal, Prince Albert
SAM	South African Museum, Cape Town
SMC	Sedgewick Museum, Cambridge
SU	Geological Collections, Stellenbosch University

SYSTEMATICS

Order PROETIDA Fortey & Owens, 1975

Superfamily PROETACEA Salter, 1864

Family **Dechenellidae** Přibyl, 1946

Genus ***Ormistoniella*** gen. nov.

Type species *Proetus malacus* Lake, 1904;
by original designation herein

Etymology

For Allen R. Ormiston of Amoco Production Company, Tulsa, who assisted the writer with literature pertaining to this species and who has contributed greatly to an understanding of the dechenellid trilobites.

Diagnosis

Cephalon semicircular with very prominent, long, genal spines. Glabella pear-shaped, tapering anteriorly. Glabellar furrows weak to obsolete; 1p deepest, with weak adaxial branches tending to isolate L1. Preglabellar field lacking. Eyes large, crescentic, close to axial furrows. Facial sutures strongly divergent anteriorly. Thorax with 9 segments. Pygidium macropygous, oval, elongate, with narrow but distinct border. Axis with 14–16 rings and pleural fields with 6–7 pairs of ribs. There is a short post-axial field.

Discussion

Ormistoniella gen. nov. differs from *Dechenella (Dechenella)* in having less deeply incised glabellar furrows, lacking a marked angulation of the anterior facial sutures at the border furrow, possessing only 9 thoracic segments, and with a pygidium with only 6–7 ribs in the pleural field and a very narrow post-axial border. It is perhaps closest to *D. (Basidechenella)* which it resembles in the shallowness of the glabellar furrows and very weak preoccipital lobes, but may be distinguished by fewer thoracic segments and pleural ribs to the pygidium and with a much narrower pygidial border. *Ormistoniella* may be distinguished from *D. (Monodechenella)* by its pear-shaped glabella and fewer pleural ribs to the pygidium.

It is clear from the above that *Ormistoniella* gen. nov. is closely allied to *Dechenella* and that the differences may warrant only subgeneric separation, a procedure originally favoured by the writer. However, in view of the constancy of the count of 10 thoracic segments in all other known dechenellids, the presence of only 9 in *Ormistoniella malacus* seems to be meaningful taxonomically. As such the differences are herein considered sufficient for generic separation.

Ormistoniella malaca (Lake, 1904)

Figs 1–4, 5C, 6B, 7C

Praetus ricardi Schenk, 1888: 227 (*nomen nudum*).
Proetus malacus Lake, 1904: 213, pl. 25 (fig. 10). Reed, 1925*a*: 119, pl. 11 (fig. 3).
Proetus ricardi Schenk, Schwarz, 1906: 390, pl. 10 (fig. 5).
Dechenella? malaca (Lake) Eldredge & Ormiston, 1979: 164.

Material

The holotype, by monotypy, SAM–K559, together with SAM–PDB 4203, AM–35, SU–K460, RO–8, 412, 748, 759–761, 830, 832, P55–56, C27, E4, 13, 63, 68, PRV–26, 71, and an unnumbered KM specimen.

Description

Cephalon. The cephalon is semicircular, much wider than the sagittal length, and with long genal spines extending backward as far as the 5th or 6th thoracic segment. The lateral and anterior borders are broad, well developed,

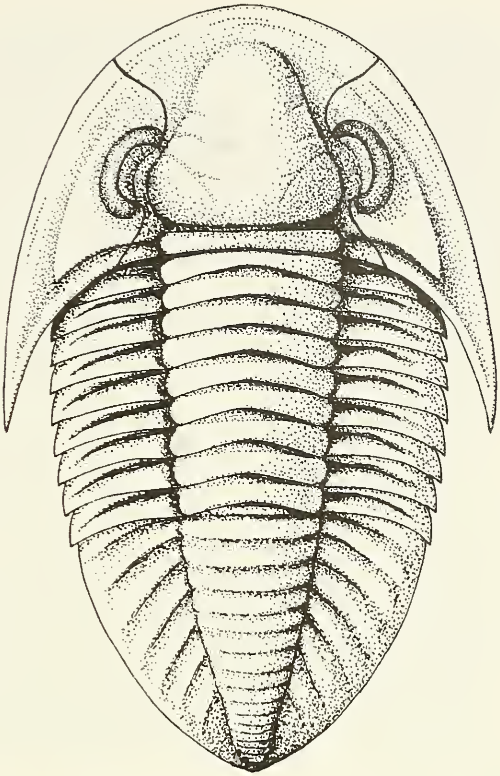

Fig. 1 *Ormistoniella malaca* (Lake).
A reconstruction based upon the available material. × 2.

and striated along their lengths. The rather shallow lateral border furrows meet the moderately deep posterior border furrows in very acute angles at the bases of the genal spines and are produced backward almost to their distal tips. The occipital furrow is narrow and deep, and the occipital ring is of uniform width. The glabella is urceolate, waisted opposite the 3p furrows, very broad and short with a maximum transverse width slightly less than the sagittal length, and tapers rather strongly to the anterior. The axial furrows are shallow, especially opposite the eye lobes. Glabellar segmentation is poorly developed; 3p is faint, very short, and almost normal to the glabellar margin; 2p is slightly longer and weakly curved but equally indistinct; 1p is the deepest, but still weakly developed, and curves back almost to the occipital furrow, so as to separate a subtrigonal, incipient preoccipital glabellar lobe (L1). The 1p furrows show a faint but distinct adaxial bifurcation. The glabella reaches to the anterior furrow and there is no preglabellar field. The eyes are fairly large, holochroal, and comprise hundreds of extremely small ocelli arranged in diagonal rows.

Fig. 2. *Ormistoniella malaca* (Lake). The holotype, by monotypy, SAM–PDB559, preserved as an internal mould. Note the broad pygidial axis. × 1,7.

Thorax. The thorax comprises 9 segments only (Fig. 7C) with a well-defined, strongly convex axis. The pleural fields are strongly down-turned distally, with well-defined fulcra. There are deep, prominent pleural grooves to the pleurae, which are separated by finer interpleural furrows.

Pygidium. Large, macropygous, oval in outline, and somewhat wider than the sagittal length. As with the British dechenellids (cf. Selwood 1965) there are two morphotypes amongst the pygidia, the differences perhaps reflecting sexual dimorphism. In the Type I pygidia (Fig. 3D) the moderately convex axis is rather broad, tapering fairly rapidly to the posterior, and comprises 14–16 distinct axial rings. In the Type II pygidia (Fig. 7C), the axis is relatively much narrower, more convex and tapers less strongly to the posterior. In both types, the pleural fields are moderately convex, subtrigonal, down-turned distally and with 6–7 prominent ribs separated by equally broad pleural furrows. The pleural ribs become obsolete distally so as to leave a narrow, smooth border with an entire margin. There is a narrow post-axial field which is terminally acuminate.

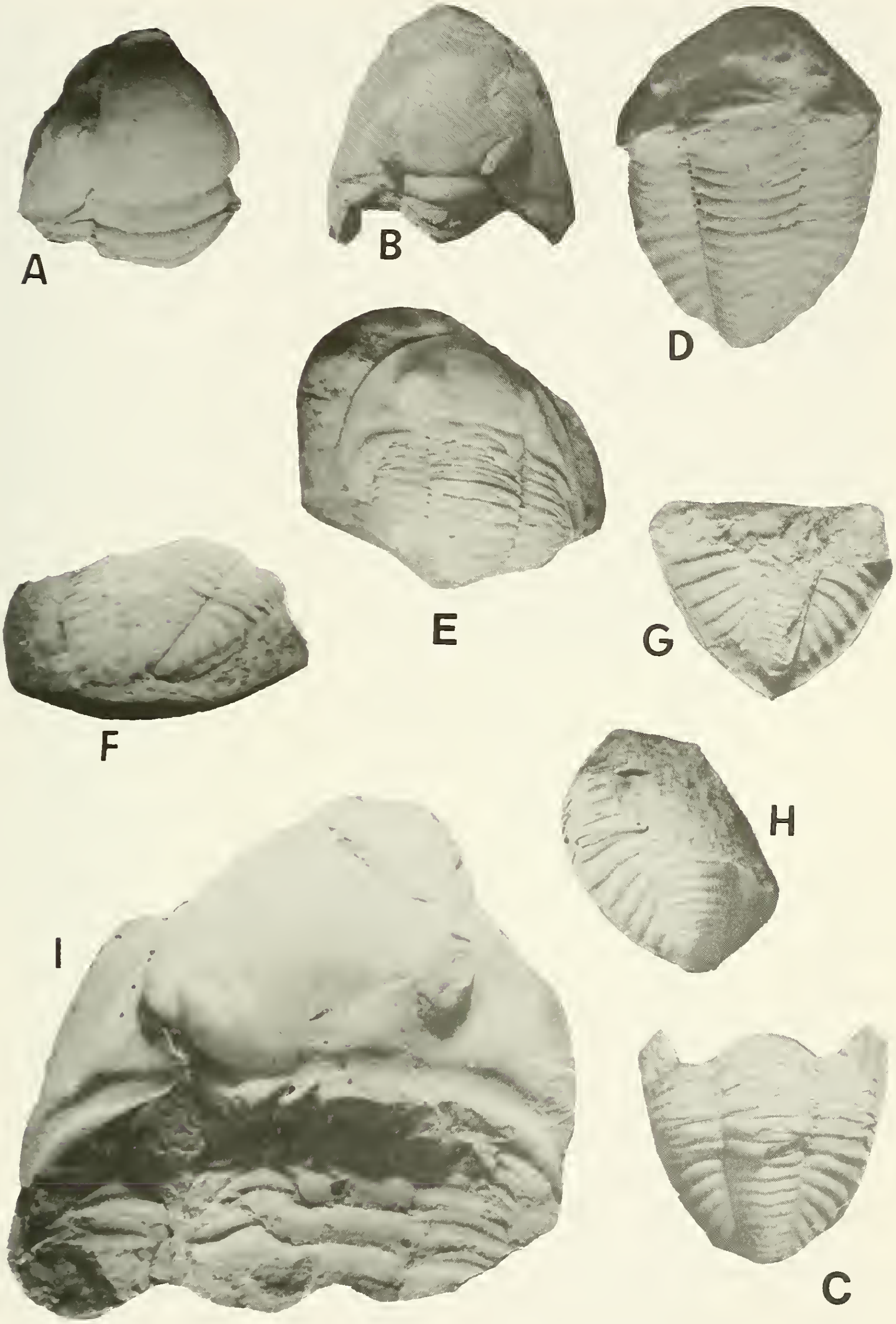

Fig. 3. *Ormistoniella malaca* (Lake). A. RO–760. B–C. RO–748, an enrolled specimen. D. RO–761. Note the broad pygidial axis. E–F. An enrolled specimen, unnumbered, in the Alexander MacGregor Museum. G. RO–P55. H. RO–P56. I. RO–90, an unusually large individual. All preserved as internal moulds and all × 1.

Fig. 4. *Ormistoniella malaca* (Lake). Lateral view of RO–8, preserved as an internal mould. × 3.

Discussion

No other dechenellids are currently recorded from the Malvinokaffric Realm and hence *O. malaca* is easily distinguished. '*Proetus*' *hexensis* Reed (1925*a*: 121, pl. 7 (fig. 8)) is based upon pygidia which differ from *O. malaca* in being semicircular in outline, with fewer axial rings and pleural ribs, indistinct segmentation and a distinct post-axial field.

'*Proetus*' *problematicus* Swartz (1925: 56, pl. 1 (figs 3–5)) is based upon fragmentary material from Bolivia that shows this species to be micropygous and thus probably an otarionid. *Dechenella (Basidechenella?) boteroi* Caster & Richter (*in* Richter & Richter 1950: 161; Eldredge & Ormiston 1979: 164) from the Devonian Floresta Beds of Colombia has median tubercles to the axial rings of the pygidium, 9 pairs of pleural ribs that are also tuberculate, and a broad, flattened border and hence is not liable to be confused with the present species.

'*Proetus*' *chengi* Sun (1937: 350, pl. 1 (fig. 2)) from the Upper Devonian Hsikuangshan Formation of Hunan, China, resembles *O. malaca* in the outline and narrow border of the pygidium, and with '13 or more' axial rings, but its axis tapers more rapidly to the posterior and there are said to be 12 pairs of ribs in the pleural fields.

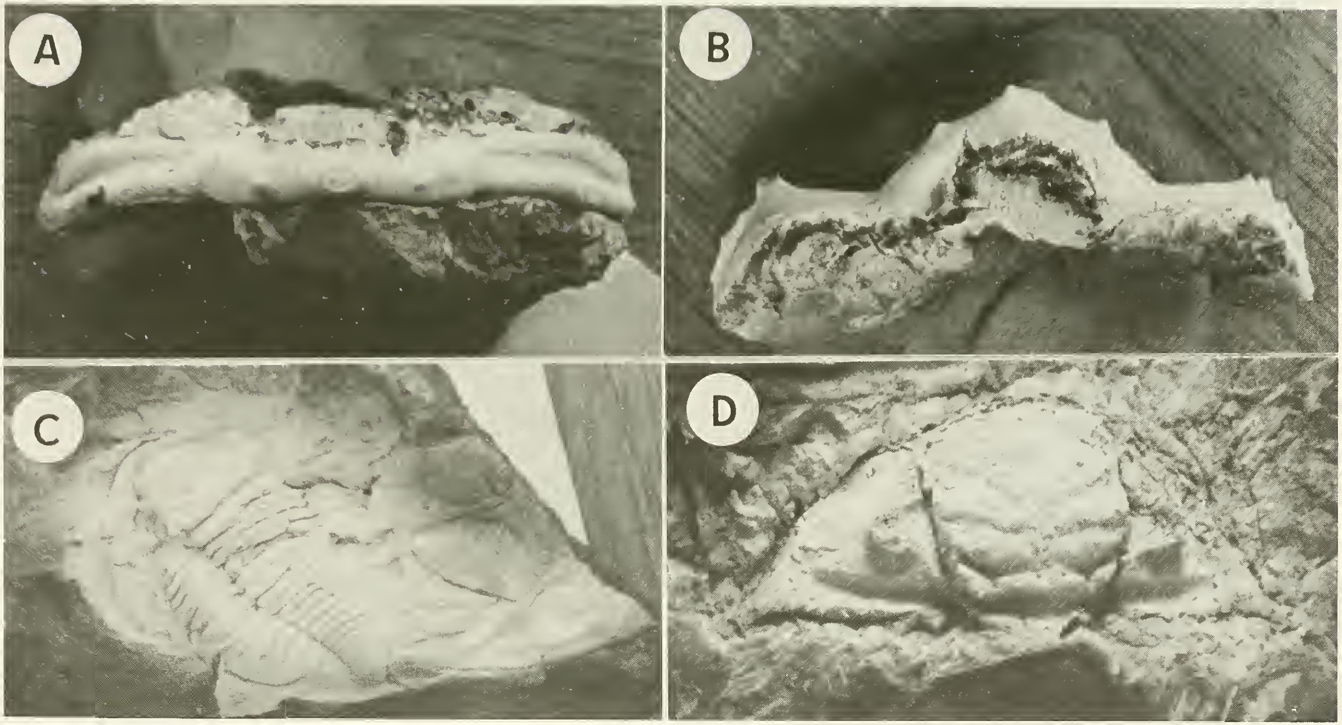

Fig. 5. A–B. *Bainella arbuteus* (Lake). RO–785, an isolated thoracic segment preserved as an internal mould. Note prominent spine bases at fulcral axes. ×1,5. C. *Ormistoniella malaca* (Lake). SU–K460, an internal mould of an ecdysized moult. ×1. D. *Bainella cristagalli* (Woodward). RO–C77, an internal mould. Note the long genal spines. ×2.

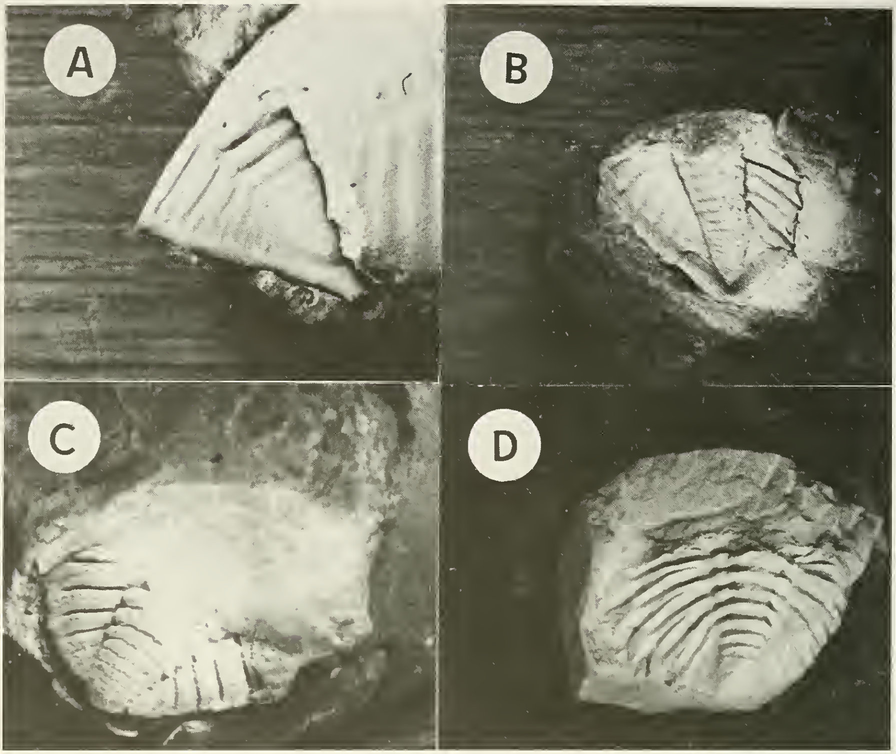

Fig. 6. A. *Deltacephalaspis pseudoconvexus* (Reed). The lectotype, designated herein, SAM–7201, preserved as an internal mould. × 1,9. B. *Ormistoniella malaca* (Lake). SAM–PDB4203, preserved as an internal mould. × 1,2. C. *Pennaia pupillus* (Lake). SAM–9605, preserved as an internal mould. × 2. D. *Metacryphaeus caffer* (Salter). SAM–PDB4347, an internal mould. × 1,1.

Boliviproetus branisai Eldredge & Ormiston (1979: 163, pl. 1 (figs 1–7)) has a strongly inflated cephalon with a narrow preglabellar field. The strongly inflated glabella is oval in outline, not urceolate as in *O. malaca*. The pygidium of *B. branisai* is readily distinguishable from that of *O. malaca* in its weak axial segmentation and effaced axial furrows, with all but the first interpleural furrows obsolete.

Dechenella clara (Hall) (Hall & Clarke 1888: 104, pl. 20 (figs 12–14), pl. 22 (figs 28–30)) from the Onondaga Limestone bears a general resemblance to *O. malaca*, but possesses pronounced occipital lobes and a pygidium twice as wide as long, with 7–11 axial rings and 4–5 pleural ribs.

Dechenella mackayi Allan (1935: 27, pl. 1 (fig. 2)) from the Reefton Beds of New Zealand resembles *O. malaca* in its multisegmented pygidial axis with 12–15 axial rings and pleural fields with 7–8 pairs of ribs. It differs, however, in having an elliptical outline to the pygidium, pleural ribs that are much wider

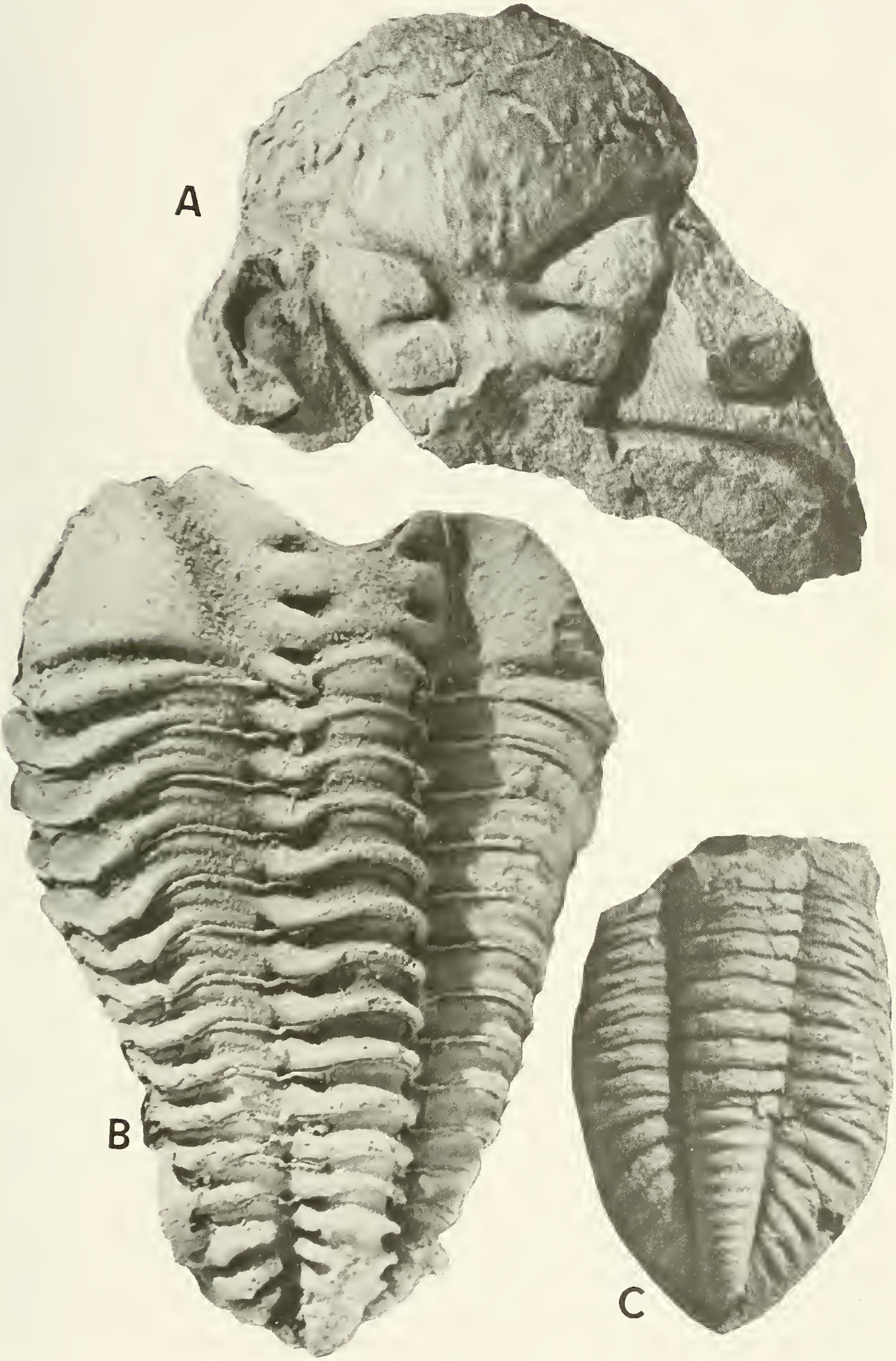

Fig. 7. A. *Gamonedaspis boehmi* (Knod). PRV–126a, an internal mould. ×2,6. B. *Typhloniscus baini* (Salter). PRV–625, preserved as an internal mould. ×2,4. C. *Ormistoniella malaca* (Lake). PRV–71, an internal mould. Note nine segments to thorax and narrow pygidial axis. ×3.

than the intervening furrows and with distinct pleural grooves, and in possessing granulose ornament.

Occurrence

Ormistoniella malaca (Lake) is common in the Gydo Formation, while a single specimen, PRV–26, in green shale preservation may be from the Voorstehoek Formation.

Family **Otarionidae** Richter & Richter, 1926

Subfamily Otarioninae Richter & Richter, 1926

Genus *Malimanaspis* Baldis & Longobucco, 1977

Type species *Malimanaspis sarudianskii* Baldis & Longobucco;
by original designation

Malimanaspis? dereimsi (Kozlowski, 1923)

Fig. 8

Cyphaspis dereimsi Kozlowski, 1923: 61, pl. 4 (figs 15–17). Swartz, 1925: 34. Reed, 1925*a*: 12, pl. 10 (fig. 10).
Otarion dereimsi (Kozlowski) Braniša, 1965: 96, pl. 16 (figs 29–30).
Otarion (Maurotarion) dereimsi (Kozlowski) Eldredge & Ormiston, 1979: 165.
Malimanaspis dereimsi (Kozlowski) Baldis & Longobucco, 1977*a*: 154.

Material

SMC–A3062*a*, obtained from a road cutting between De Doorns and Tunnel (Reed 1925*a*), is still the only example known from the Bokkeveld Group.

Description

Cephalon. The cephalon is semicircular, with the anterior border slightly pointed sagittally, about twice as wide as the sagittal length, and with prominent genal spines extending backward to about the fourth thoracic segment. There is a well-developed preglabellar field, with a broad, fairly deep anterior furrow and a convex anterior border. The lateral borders to the cephalon are also very broad. The glabella is strongly inflated, trapezoidal in outline, almost rectangular, with maximum width at the occipital furrow. The deep, well-developed 1p glabellar furrows curve strongly backward to separate pronounced pre-occipital lobes (L1). L1 is half the exsagittal length of the glabella, whilst the 2p and 3p furrows are obsolete. The glabella is surrounded by deep, narrow axial and preglabellar furrows. The occipital furrow is rather narrow, anteriorly convex, and separates off an occipital ring of constant width. Although the eyes are missing from the present specimen, their broken bases suggest they were moderately large. The anterior branches of the facial suture are strongly divergent and the posterior branches extremely so, the latter meeting the posterior margin somewhere in the genal spines.

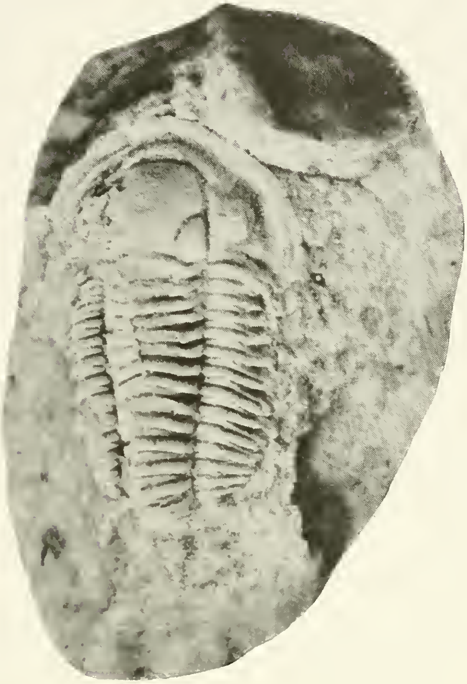

Fig. 8. *Malimanaspis? dereimsi* (Kozlowski). SMC–A3062a, preserved as an internal mould. × 1,6.

Thorax. The thorax comprises at least 12 segments and has a broad axis, about one-third of the thoracic width. The pleurae bear deep pleural grooves and display prominent fulcra.

Pygidium. Unknown from the present material.

Discussion

The generic assignment of the Bokkeveld specimen poses some problems. It was regarded as conspecific with the South American *Cyphaspis dereimsi* Kozlowski both by Reed (1925*a*) and the writer. However, Baldis & Longobucco (1977*a*) have recently assigned Kozlowski's species to their new genus *Malimanaspis*, distinguished by a pustulose ornament over the entire exoskeleton, which is reflected on internal moulds, the presence of a median tubercle to the occipital ring, and median tubercles (spines?) to the thoracic axial rings, and a pygidium with less than 5 axial rings. Kozlowski (1923) makes no mention of pustulose ornament in his original description of *Cyphaspis dereimsi*, nor of the presence of a median tubercle to the occipital ring or sagittal tubercles to the thoracic axis. Similarly, none of these features is evident in the

Bokkeveld specimen, although the writer does not have the original for close inspection. The cranidium figured by Wolfart (1968, pl. 1 (fig. 1)) and assigned to *Otarion dereimsi* does, however, show pustulose ornament but, since there are now known to be at least 2 species of otarionid in the Malvinokaffric Realm, is perhaps better referred to *Malimanaspis sarudianskii* Baldis & Longobucco. Clearly the problems surrounding *Otarion dereimsi* (Kozlowski) can be resolved only by a restudy of the type material. The Bokkeveld example is, therefore, only questionably assigned to the genus *Malimanaspis*, since it also resembles *Otarion (Maurotarion)*.

Amongst Bokkeveld species, the only possibility of confusion of *Malimanaspis? dereimsi* lies with *Ormistoniella malaca* (Lake). The latter species has, however, an urceolate glabella that lacks the deep 1p furrows and well-developed pre-occipital lobes of *Malimanaspis? dereimsi*, as well as being macropygous.

Otarion (Maurotarion) maurum (Alberti) (1967: 500, pl. 1 (fig. 28); 1969: 384, pl. 36 (figs 1–4), pl. 46 (fig. 19)) is a Silurian (Lower Ludlow) species from Morocco which differs from *M? dereimsi* in having relatively smaller pre-occipital lobes, convex axial furrows to the glabella, a more strongly convex preglabellar furrow, and a sagittal node to the occipital ring. *Otarion (Maurotarion) neptis* (Alberti) (1969: 386, pl. 36 (figs 9–10)) is easily separated from the present species by its elliptical glabella with relatively much smaller pre-occipital lobes and much broader occipital ring with a sagittal node. These are also much the same features that distinguish *O. (M.) ambiguum* (Alberti) (1969: 388, pl. 36 (fig. 11)), which also has a narrower anterior border not weakly pointed sagittally as in *M? dereimsi*. *Otarion (Maurotarion) elegantulum* (Loven) (Alberti 1969: 384, pl. 36 (figs 5–6)) is a Silurian species with a pronounced anterior border, which is distinctly pointed on the sagittal line, and with a strongly convex preglabellar furrow, relatively smaller pre-occipital lobes, and a much broader occipital ring than the present species. Other species referred to *O. (Maurotarion*) by Alberti (1969) include *O. (M.) novellum* (Barrande), *O. (M.) institia* Whittington & Campbell, *O. (M.) plautum* Whittington & Campbell, *O. (M?) cristyi* (Hall), and *O. (M?) girardeauensis* (Shumard), but the writer does not have access to the literature pertaining to these species.

Kozlowski (1923) and Eldredge & Ormiston (1979) have pointed to the similarity of this species with *Otarion miniscula* Hall (Hall & Clarke 1888: 140, pl. 24 (figs 7–12)) from the Bois Blanc, Schoharie, and Onondaga of Ontario and New York, from which it was distinguished by its larger size and stouter genal spines.

Otarion tiaomachienensis (Sun) (1937: 349, pl. 1 (fig. 1)) has much smaller pre-occipital lobes than the present species and its glabella is more strongly inflated anteriorly, with a strongly convex preglabellar furrow.

'*Proetus*' *problematicus* Swartz (1925: 56, pl. 1 (figs 3–5)) may be an otarionid; it shows a small, subtrigonal pygidium that differs from that of the present species in lacking trilobation and segmentation. The *Cyphaspis* sp. of

Kozlowski (1923: 62, pl. 4 (fig. 18)) was assigned to *Andinacaste legrandi* sp. nov. by Eldredge & Braniša (1980).

Eldredge & Ormiston (1979) refer to a second species of *Otarion* in the Belen Beds of Bolivia, which was said to show considerable resemblance to *O. (M.) novellum* (Barrande). It was distinguished from *M. dereimsi* by its semicircular cephalon and slender genal spines, relatively smaller pre-occipital lobes, convex preglabellar furrow, narrow anterior and lateral borders, and median node to the occipital ring. It must also, therefore, be very close to *O. (M.) ambiguum* (Alberti).

Occurrence

Malimanaspis? dereimsi (Kozlowski) ranges from the zone of *Bainella insolita* through to the *Metacryphaeus giganteus* Zone in Bolivia, but its level of occurrence in South Africa is uncertain.

Order PHACOPIDA Salter, 1864

Suborder CALYMENINA Swinnerton, 1915

Family **Homalonotidae** Chapman, 1890

Subfamily Homalonotinae Chapman, 1890

Genus *Burmeisteria* Salter, 1865

Type species *Homalonotus herscheli* Murchison, 1839;
by original designation

Discussion

Two subgenera are currently recognized in this genus; they are *Burmeisteria (Burmeisteria)* with a supposedly urceolate glabella showing distinct lobation and a biconcave rostral suture, and *B. (Digonus)* in which the trapezoidal glabella lacks lobation and the rostral suture is transverse or slightly concave. However, as remarked by Sdzuy (1957) and Saul (1965), the form of the rostral suture is highly variable and thus of little taxonomic significance. This is confirmed by the present study, which suggests its form may in part be ontogenetically related and that the shape of the glabella and the strength of its lobation cannot be used to distinguish *B. (Burmeisteria)* and *B. (Digonus)*. Indeed, available material of *B. herscheli*, the type of the genus, shows every transition between these two subgenera and at this level the criteria on which they were established do not appear to be of specific let alone subgeneric importance. Consequently, the subgenus *Digonus* is herein considered a junior subjective synonym of *Burmeisteria* s.s.

In providing the most recent discussion of this subfamily, Thomas (1977) pointed to the similarity of the cephalon of *Burmeisteria* with that of juvenile *Dipleura* and suggested that *Burmeisteria* may be a neotenous descendant of *Dipleura*.

Saul (1965) has suggested that this genus may be dimorphic, the dimorphs distinguished by the characters of the pygidium. If present in *B. herscheli* (Murchison), any such dimorphism is certainly inconspicuous and masked by polymorphism.

Burmeisteria herscheli (Murchison, 1839)

Figs 9–13, 14A–B, D–F, 15–28, 39E, 56H

Homalonotus herscheli Murchison, 1839: 652, pl. 7 (fig. 2). Salter, 1856: 215, pl. 24 (figs 1–8). Lake, 1904: 214, pl. 26 (figs 1–3). Schwarz, 1906: 383, pl. 8 (fig. 8), pl. 9 (fig. 3). Clarke, 1913: 93, pl. 3 (figs 1–4).
Homalonotus perarmatus Frech, 1897: 218.
Homalonotus quernus Lake, 1904: 216, pl. 27 (fig. 1).
Homalonotus colossus Lake, 1904: 216, pl. 28 (figs 1–3).
Homalonotus sp., Lake, 1904: 217, pl. 27 (fig. 2).
Homalonotus herscheli Salter var?, Schwarz, 1906: 383, pl. 8 (fig. 8).
Homalonotus horridus Schwarz, 1906: 385, pl. 9 (fig. 1).
Homalonotus agrestis Schwarz, 1906: 386, pl. 9 (fig. 2).
Homalonotus hippocampus Schwarz, 1906: 388, pl. 9 (fig. 5).
Homalonotus lex Schwarz, 1906: 389, pl. 9 (fig. 4).
Homalonotus (Burmeisteria) herscheli Murchison, Reed, 1918: 314; 1925*a*: 163.
Homalonotus (Burmeisteria) herscheli var. *rectisuturalis* Reed, 1925*a*: 167, pl. 10 (figs 3, 7).
Homalonotus (Burmeisteria) herscheli var. colossus Lake, Reed, 1925*a*: 169.
Homalonotus (Burmeisteria) herscheli var. fusiformis Reed, 1925*a*: 171.
Homalonotus (Burmeisteria) herscheli var. *grahami* Reed, 1925*a*: 172.
Homalonotus (Burmeisteria) herscheli var. *bituberculata* Reed, 1925*a*: 173, pl. 10 (fig. 2).
Homalonotus (Burmeisteria) herscheli var. *perarmata* Frech, Reed, 1925*a*: 175.
Homalonotus (Burmeisteria) quernus Lake, Reed, 1925*a*: 181, pl. 9 (fig. 13), pl. 10 (fig. 1).
Homalonotus (Burmeisteria?) hippocampus Schwarz, Reed, 1925*a*: 183.
Homalonotus (Burmeisteria) sp., Reed, 1925*a*: 184.
Burmeisteria herscheli (Murchison) Saul, 1965: 271.
Burmeisteria hippocampus (Schwarz) Sdzuy, 1957: 283, fig. 1.
? Burmeisteria herscheli (Murchison) Braniša, 1965: 84, pl. 10 (figs 1, 4), pl. 11 (fig. 6).
? Burmeisteria (Burmeisteria) sp., Wolfart. 1968: 61.

Material

Salter's (1856) original material in the British Museum, abundant material in the South African Museum including SAM–7199, SAM–PDB598, 600, 619, 626–627, 1406, 4292–4293, 4343, 4345, 4352, 4356, 4359, 4360–4364, 7193, 7201, 7795–7796, SU–C6, D182, K810, AM–1–2, 6, 8, 13, 21, 61–64, 1432, 1444, 1457, 1462, 1613, 1616, 2552–2554, together with RO–16, 175, 257, 271, 807–808, 810–812, 815–819, 825, E22, 50–52, 57–59, 72, 90–92, L20, 60, and 93.

Description

Cephalon. The cephalon is moderately to very convex (depending on the size and the nature of preservation), with downturned cheeks and a subtrigonal to trapezoidal outline. It is wider than the sagittal length, with a prominent occipital furrow and fairly deep posterior border furrows that shallow abaxially.

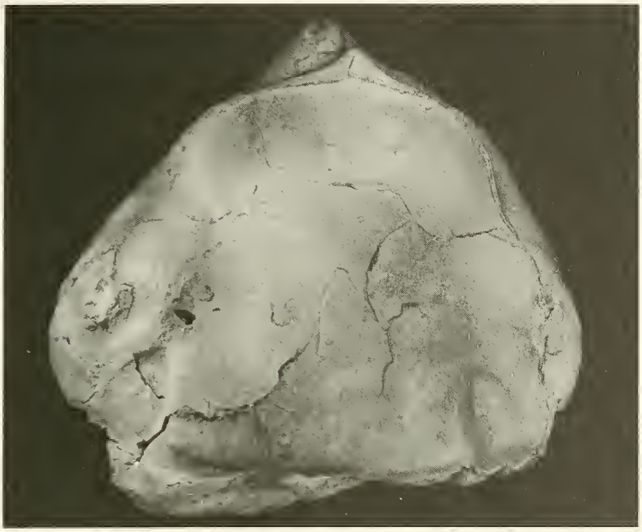

Fig. 9. *Burmeisteria herscheli* (Murchison). The original of Salter (1856, pl. 24 (fig. 1)), preserved as an internal mould. × 1.

The lateral border furrows are very shallow and indistinct and there is no anterior border furrow, although the whole of the preglabellar field is gently concave. The preglabellar field is moderately broad, generally between 17–20 per cent of the sagittal length of the cephalon, and may be flattish or distinctly upturned. The glabella is very slightly elevated and generally subtrapezoidal in outline, though tending to urceolate in some individuals. The axial furrows are moderately deep, diverging slightly to the posterior, whilst the anterior margin of the glabella is abruptly truncate but still with rounded corners and a gently convex preglabellar furrow. Glabellar segmentation is variably developed from individual to individual, tending to be most pronounced in juveniles and commonly very weak or obsolete in the middle and adult growth stages. The 3p furrows are weak to indistinct, short, directed posteromedially and subparallel to the slightly longer and more pronounced 2p furrows. The 1p furrows are strongly curved adaxially, almost reaching the occipital furrow and tending to separate weakly developed, subtrigonal, pre-occipital lobes. The occipital furrow is transverse, sometimes arched forward sagittally, and commonly narrower than the occipital ring. The posterior borders broaden slightly abaxially and commonly bear from 1 to 3 small dorsal spines (Fig. 22) just before the rounded genal angles. The subtrigonal paraglabellar areas (Fig. 9) vary from indistinct to prominent, tending to be more pronounced in larger individuals. In some examples the paraglabellar areas tend to invade the L1 lobes, giving them slightly concave lateral margins. The strongly convex cheeks bear prominent rounded bosses on top of which are situated the small elevated eyes surrounded by shallow circumocular furrows. The eyes are situated just posterior to the abaxial terminations of the 2p glabellar furrows. The rostral plate is triangular, varying from equilateral to distinctly longer (sag.) than wide, and bears a prominent, hooked, beak-like, median spine. The hypostoma (Fig. 39E) is similar to that of *Homalonotus* but with only a very weak posterior indentation. The facial suture is proparian, the posterior branches cutting the lateral margins just in front of the genal angles. The anterior facial suture is highly variable, with the rostral suture either transverse, concave or biconcave. This character may be ontogenetically related (Fig. 23) since small individuals generally have a concave rostral suture, while a biconcave suture is encountered only in moderately large to large specimens. The entire surface of the cephalon is granulose, with randomly scattered tubercles (Fig. 24) that vary in distribution from individual to individual, but tend to be concentrated along the posterior borders.

Thorax. The thorax comprises 13 segments with a very broad axis, which is at least 60 per cent of the thoracic width. Ornament comprises scattered granules and randomly distributed tubercles (Fig. 25), the latter tending, however, to form a longitudinal row just inside the axial margins. As shown by SAM–K1406, the tubercles represent spine bases (Fig. 56H). The axial furrows are indistinct but marked by prominent pits at the adaxial ends of the interpleural furrows. The pleural furrows are deep, diverging abaxially from the anterior borders of the pleurae (Fig. 17D), and terminate just before the truncate distal margins of the pleurae.

Pygidium. The pygidium is strongly convex, triangular, longer than wide, and with fairly distinct trilobation. The axis is triangular, rather broad anteriorly but tapering to the posterior and terminating before the posterior margin is reached to leave a short post-axial field. In large individuals the axis comprises 16–17 rings, with the segmentation tending to become indistinct for the last few rings. On internal moulds the terminal point of the pygidium is sharply rounded, acuminate. The axial rings are much wider than the ring furrows and may, or may not, bear a few scattered tubercles (Figs 25–26), while the entire cuticular surface of the pygidium is granulose. The pleural fields are triangular, convex, and curved almost vertically downwards at their margins. They are commonly ornamented with 9–11 pairs of low ribs that are wider than the interpleural furrows. The ribs do not reach the lateral margins, leaving a narrow entire border. The pleural grooves vary from very indistinct to obsolete.

Discussion

Since a species is defined on the basis of the characters of a population of individuals, it is clear that the thirteen or so taxa of *Burmeisteria* currently recognized in the Bokkeveld fauna represents a gross splitting of a small number of variable species. Thus, it is readily apparent that *B. herscheli* displays an extreme range of intraspecific variation and hence genetic polymorphism. This is most apparent in the characters of the tuberculation and it is worth recalling Reed's (1925*a*: 179) comment that '. . . the lack of bilateral symmetry and the general irregularity in the distribution of the tubercles and spine bases on the thorax and pygidium is a noticeable feature in all the forms here regarded as varieties of *H. Herscheli*, and for this reason the tuberculation must be regarded as of small specific or varietal value. Individuals, otherwise identical, differ considerably in this respect'. The author agrees wholeheartedly with this statement although the varietal rank is here used only for recurring morphotypes that form a significant percentage of the individuals within a contemporaneous population. With regard to the rostral suture, it has already been noted that its form seems to be ontogenetically related and it is not herein considered of specific importance. Similarly, the strength of the glabellar segmentation is so variable, depending on ontogenetic stage and mode of preservation, that it, too, does not appear to be of taxonomic importance among the present material.

Burmeisteria herscheli was originally based upon a thorax and pygidium (Murchison 1839, pl. 7 (fig. 2)), with the original of Salter's (1856) plate 24, figure 1 generally being regarded a typical cephalon. However, as noted by Reed (1925*a*), Salter's figure is a restoration based upon more than one individual since the original of his figure 1 (Fig. 9) lacks the occipital ring and posterior borders.

Lake (1904) introduced *Homalonotus colossus* for a very large but fragmentary cephalon that Clarke (1913: 95) considered to be merely a large *B. herscheli*. Reed (1925*a*: 170), however, felt that ' . . . it may be worthy of being a variety, for there are more numerous (5) tubercles or spine bases on the pleuro-occipital rings, and the thoracic segments bear 2 pairs of lateral spines or tubercles'. As can be seem from Figures 24–26, however, the distribution of tubercles in *B. herscheli* is highly variable and the use of this character, even at the varietal level, would result in a superfluous multiplicity of names. Consequently, the writer follows Clarke (1913) in considering *H. colossus* a junior subjective synonym of *B. herscheli*.

Homalonotus quernus Lake (Fig. 27A) was based upon a very large fragmentary specimen showing coarse tuberculation on the glabella and thorax. Since, however, there are transitional forms to the sympatric *B. herscheli* (Fig. 24), the differences are not herein considered of specific importance, although Lake's name may usefully be retained at the varietal level for the hypernodose individuals within *B. herscheli* populations. As suggested by Reed (1925*a*), the fragmentary pygidium figured by Lake (1904: 217, pl. 27 (fig. 2)) as a *Homalonotus* sp. (Fig. 27B) should be assigned to this variant.

Homalonotus perarmatus Frech (Fig. 20) and *H. horridus* Schwarz are both multituberculate 'species' transitional from *B. herscheli* s.s. to the var. *quernus*. Consequently, the writer would agree with Lake (1904) and Reed (1925*a*) in regarding *H. perarmatus* as a junior subjective synonym of *B. herscheli*, as well as following Reed (1925*a*) in including *H. horridus* Schwarz in the synonymy of Murchison's species. The retention of these names even at the varietal level serves little practical purpose and they are not used here.

Fig. 10. *Burmeisteria herscheli* (Murchison). The original of Salter (1856, pl. 24 (fig. 2)), in the British Museum (Natural History), preserved as an internal mould. × 1,5.

Fig. 11. *Burmeisteria herscheli* (Murchison). The original of Salter (1856, pl. 24 (fig. 4)), in the British Museum (Natural History), preserved as an internal mould. This specimen was referred to the var. *perarmata* Frech by Reed (1925*a*). × 1.

Homalonotus agrestis Schwarz (1906: 386) was distinguished by ' . . . the very rapid tapering of the pygidium and the incurved margin' but, as noted by Reed (1925*a*: 178), is so similar to *H. horridus* that it, too, is included in the synonymy of *B. herscheli*. *Homalonotus hippocampus* Schwarz was based upon a number of small cephala distinguished by their subtrigonal outlines and flat glabellae. According to Reed (1925*a*: 183), however, ' . . . the shape of the glabella, the practical absence or obsolescence of the lateral furrows on its

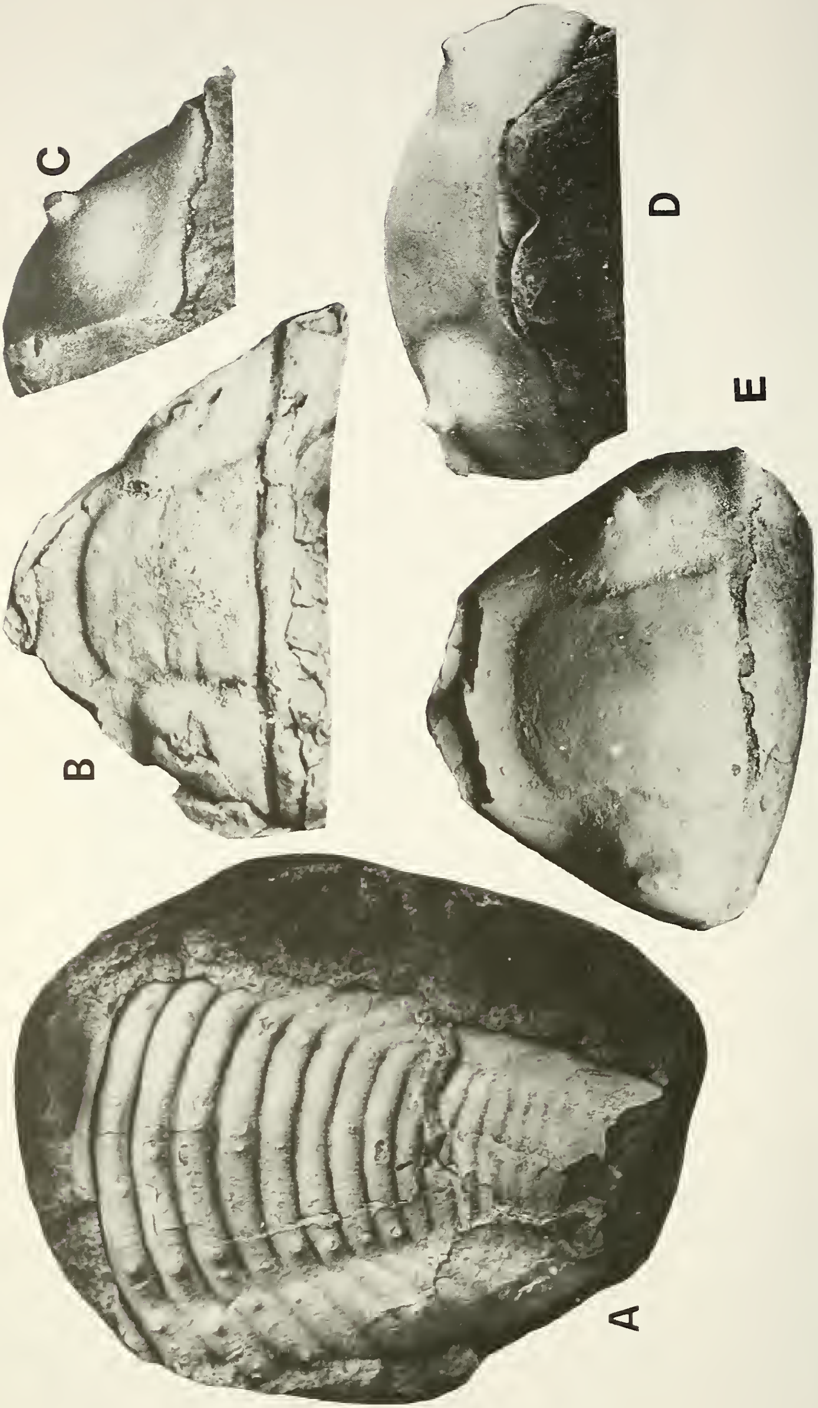

Fig. 12. *Burmeisteria herscheli* (Murchison). A. SAM–PDB4292, a pygidial fragment. B. SAM–PDB4362. Note the concave rostral suture. C–E. SAM–PDB7193, the original of Reed's 1925*a*, pl. 10 (fig. 7), referred to the var. *rectisuturalis*. All preserved as internal moulds and all × 1.

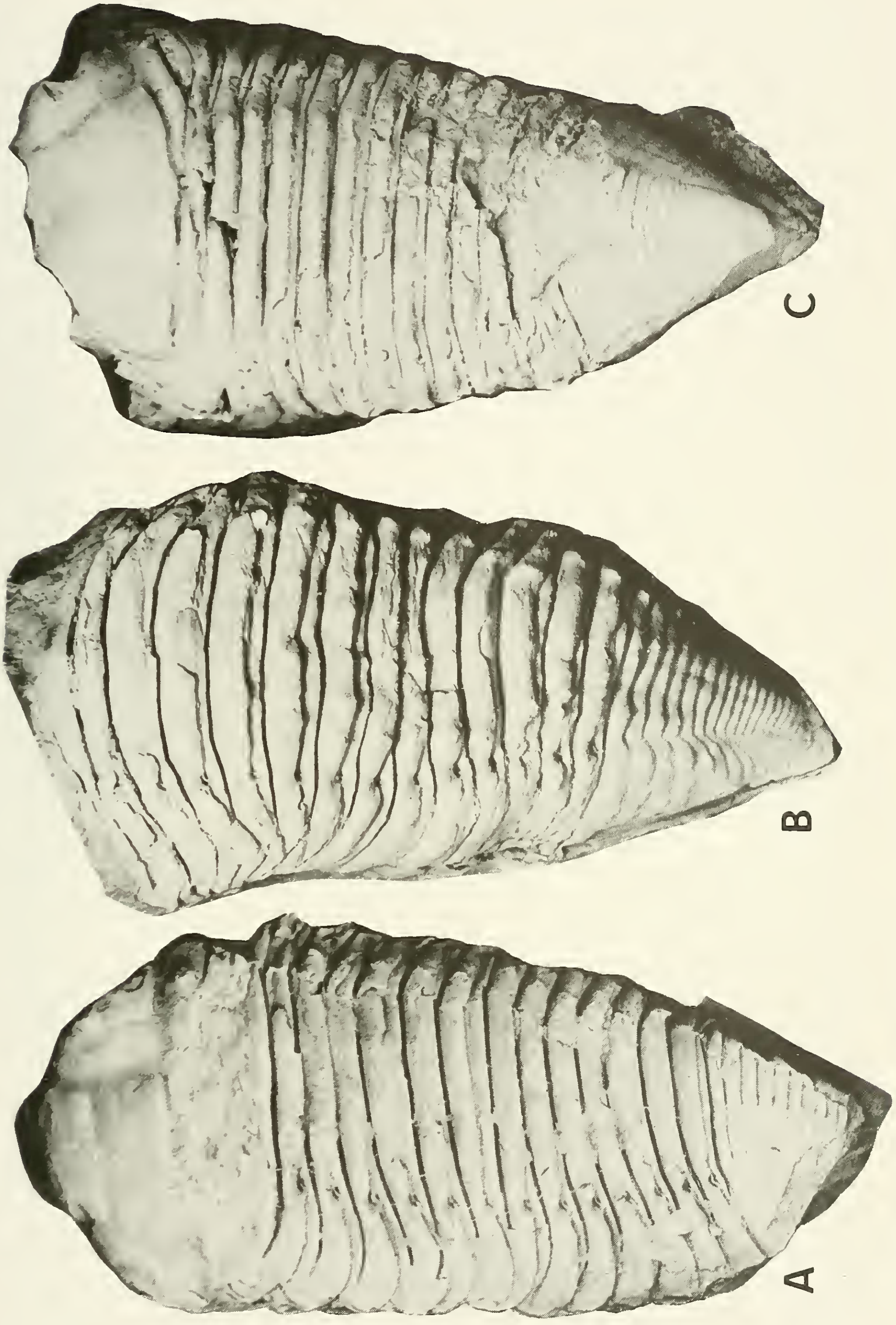

Fig. 13. *Burmeisteria herscheli* (Murchison). A. SAM–PDB4363. B. SAM–PDB4360. C. SAM–PDB7795. All preserved as internal moulds and all × 1.

surface, the straight, transverse, connecting suture in front, the presence of a pair of spine bases close to the genal angles, and other features suggest that it is only a young individual or narrow form of *H. herscheli* var. *rectisuturalis*. In the Ordovician trilobite *Ogygia buchi* Brongniart we have a narrow and a wide form, the differences being regarded as sexual. Possibly the same explanation is applicable here.' Perhaps significantly, Saul (1965) has recorded size dimorphism in *Burmeisteria antarctica* and hence Reed's opinion may be correct. In any case, the differences are not herein considered of specific importance and *Homalonotus hippocampus* is included in the synonymy of *B. herscheli.*

Homalonotus lex Schwarz was founded upon several thoracic segments (Fig. 17D) which Schwarz (1906: 389) felt might have belonged to the cephala he had named *H. hippocampus*, while noting that ' . . . the rings show no particular features differing from the usual *H. herscheli* type, except in the ends, which in *H. herscheli* are rounded in the lower margin, in this species are pointed, and probably bore spines'. The writer would agree with Reed (1925*a*) that this is an unnecessary species that should be included in the synonymy of *B. herscheli.*

Reed (1925*a*) created the var. *rectisuturalis* (Fig. 16E) within *B. herscheli* for a cephalon ' . . . which can hardly be separated specifically from *H. herscheli*, but certainly constitutes a variety remarkable for the shortness and breadth of its glabella'. The writer finds little use for this varietal name and it is not used here.

The var. *fusiformis* was created by Reed (1925*a*) for the pygidium figured by Lake (1904) (Fig. 15A–B herein) and, as the varietal name implies, distinguished by its subfusiform outline. While this variant is distinctive, no further individuals have been forthcoming and the characters seem to be those of an aberrant individual. As such, the perpetuation of Reed's name is tantamount to naming individuals and it is not used here.

Reed (1925*a*: 172) introduced the var. *grahami* (Fig. 21) for forms in which the glabella was said to be more oblong in shape and relatively longer than in typical *B. herscheli*, as well as having the cephalon more pointed anteriorly, narrower, with steeper cheeks, and with ' . . . the meso-occipital furrow more sharply bent forwards in the middle, the paraglabellar areas invade the basal lobes more deeply, and the minute ornament is slightly different, the tubercles being more numerous and closer together; the transverse suture is typically straight and not angular'. Since, however, most of these characters are also found in the 'var. *rectisuturalis*' and in '*H. hippocampus*', this variety seems to be based upon trivial differences of the individual and the name is not used here.

Burmeisteria notica (Clarke) (1913: 89, pl. 1 (figs 1–2), pl. 2 (figs 1–13)) differs from *B. herscheli* in the complete lack of tubercles and spine bases to the exoskeleton, a broader preglabellar field (about 25% of the sagittal length of the cephalon) and a pygidium with fewer (13–15) axial rings. It is perhaps also worthy of note that the pygidium figured by Clarke (1913) as plate 2, figures

11–12 shows a distinctly deeper first ring furrow than the rest. *Burmeisteria clarkei* (Kozlowski) and *B. accraensis* Saul are both very closely allied to *B. notica* and distinguished from *B. herscheli* by the complete lack of tuberculation.

Burmeisteria antarctica Saul (1965: 269, pl. 17 (figs 1–11)) (Fig. 29 herein) differs from *B. herscheli* in its lack of tuberculation, shorter rostral suture, allegedly smaller eyes and weaker glabellar segmentation, its relatively broader cephalon, and particularly in features of the pygidium. Thus, in the 'Type I' pygidia (Fig. 29) of *B. antarctica* only the anterior 7–9 axial rings are distinct and there are only 7 pairs of well-developed ribs to the pleural fields with very deep interpleural furrows. The 'Type II' pygidia are closer to *B. herscheli* in showing 12 or more axial rings, but still with only 6–7 pairs of pleural ribs.

Burmeisteria expansa (Hector) (Allan 1935: 29, pl. 1 (fig. 1)) from the Reefton Beds of New Zealand is based upon pygidia which differ from *B. herscheli* in being relatively much broader and with only 12–13 distinct axial rings and 9–12 pairs of pleural ribs. *Burmeisteria huttoni* Allan (1935: 28, pl. 1 (figs 4–5)) is from the same beds and, in view of the range of variation displayed by *B. herscheli*, probably does not warrant specific separation from *B. expansa*. So far as can be judged, *B. huttoni* differs from *B. herscheli* in that the coarse tuberculation of the thorax forms distinct transverse rows, whereas in the South African species the rows tend to be longitudinal.

Occurrence

Burmeisteria herscheli (Murchison) is presently recorded from the Gydo, Gamka, and Voorstehoek Formations of the Bokkeveld sequence, the Fox Bay Beds of the Falkland Islands and, perhaps, from Bolivia.

Burmeisteria notica (Clarke, 1913)

Figs 14C, 30

Homalonotus noticus Clarke, 1913: 89, pl. 1 (figs 1–2), pl. 2 (figs 1–13).
Homalonotus cf. *noticus* Clarke, Kozlowski, 1923: 23, pl. 1 (fig. 11).
Homalonotus sp., Kozlowski, 1923: 13, pl. 3 (figs 8–9).
?*Homalonotus (Burmeisteria) herscheli* var. *rectisuturalis* Reed, 1925*a*: 160 (SU–C1 only).
Homalonotus (Digonus) noticus var. *africana* Reed, 1925*a*: 184, pl. 10, (fig. 4).
Digonus noticus (Clarke) Sdzuy, 1957: 279.
Digonus cf. *noticus* (Clarke) Braniša, 1960: 60, pl. 6 (fig. 13); 1965: 84, pl. 10 (figs 5–7), pl. 11 (fig. 13), pl. 75 (fig. 2).
Burmeisteria (Digonus) noticus (Clarke) Saul, 1965: 271.
Burmeisteria (Digonus) cf. *noticus* (Clarke) Wolfart, 1968: 62.

Material

The holotype of Reed's var. *africana*, SAM–7796, together with RO–17, 60, 88, 174, 297 and P57, and questionably SU–C1.

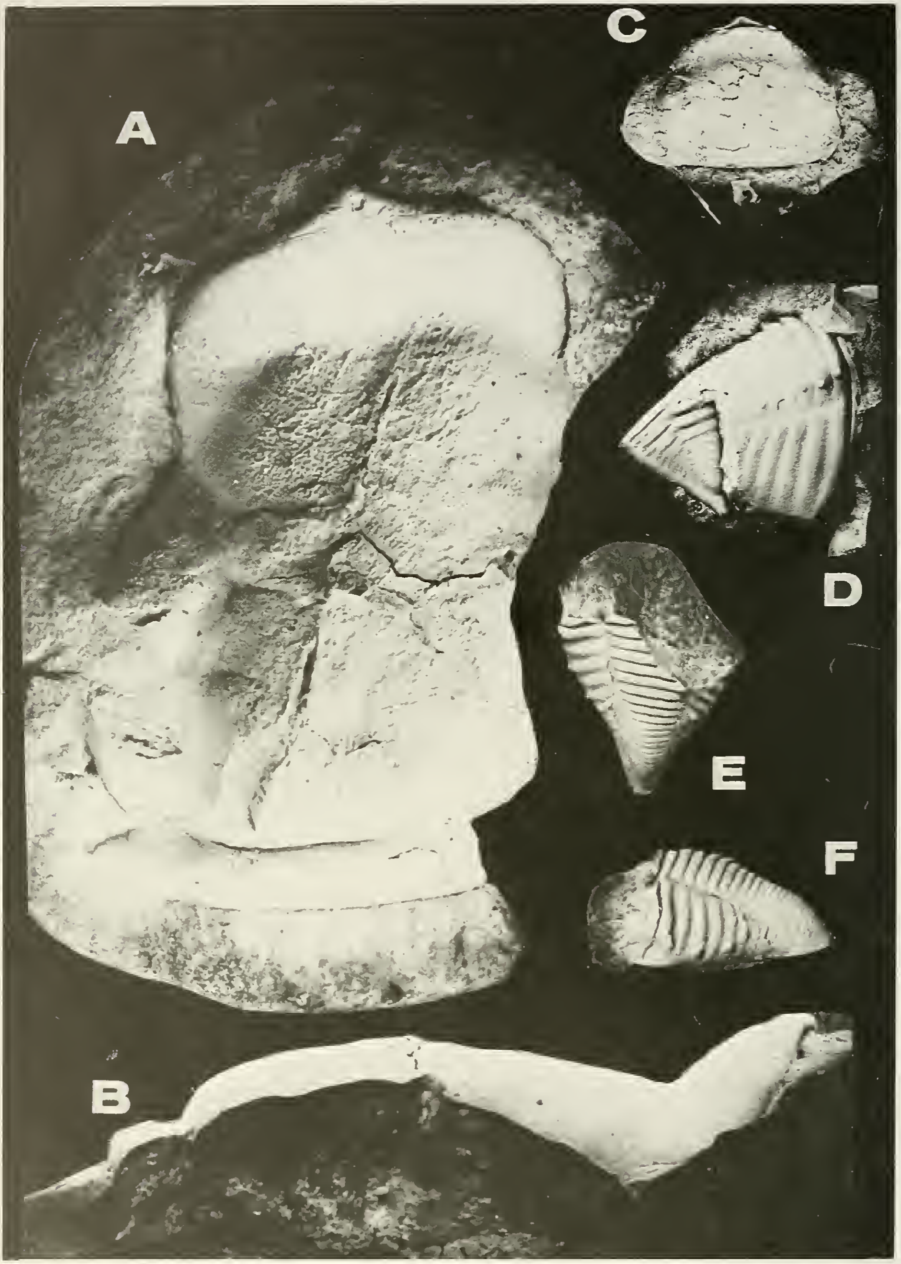

Fig. 14. A–B, D–F. *Burmeisteria herscheli* (Murchison). A–B. SAM–PDB619, the original of Lake (1904, pl. 26 (fig. 1)). D. SAM–7201, with the lectotype of *Deltacephalaspis pseudoconvexus* (Lake) impressed in its terminal portion. E–F. SAM–PDB4345. C. *Burmeisteria notica* (Clarke). SAM–7796, the holotype of the var. *africana* Reed (1925*a*, pl. 10 (fig. 4)). A–B, D–F preserved as internal moulds and all × 1.

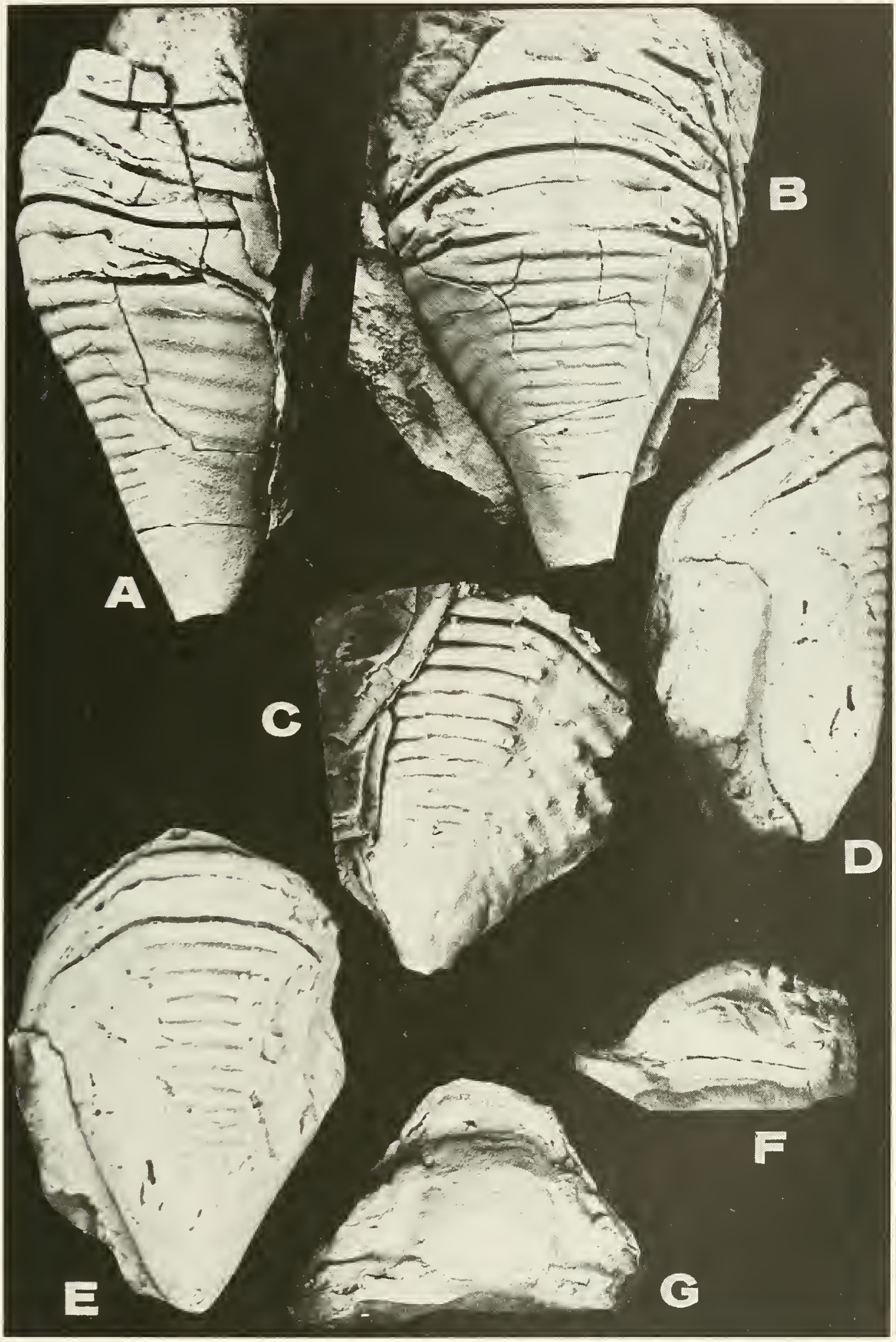

Fig. 15. *Burmeisteria herscheli* (Murchison). A–B. SAM–PDB627, the holotype of the var. *subfusiformis* Reed, figured by Lake (1904, pl. 26 (fig. 2)). C. SAM–PDB4296. D–E. SAM–PDB3075. F–G. SAM–PDB4353. All preserved as internal moulds and all × 1.

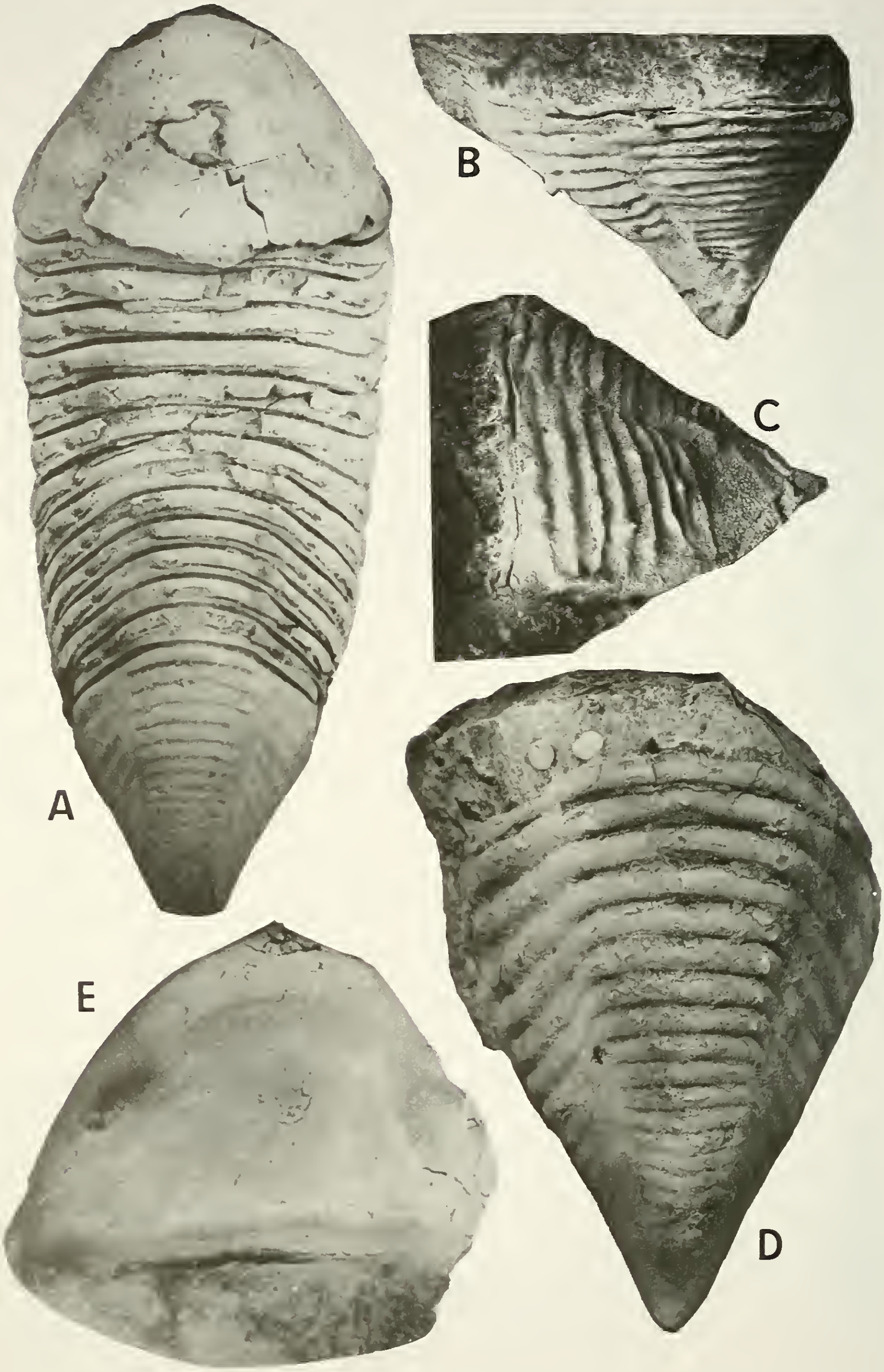

Fig. 16. *Burmeisteria herscheli* (Murchison). A. SU–K810. B–C. A tectonically foreshortened pygidium in the South African Museum. D. The original of Salter (1856, pl. 24 (fig. 7)), in the British Museum. E. SU–C6, figured by Reed (1925*a*, pl. 10 (fig. 3)) as the var. *rectisuturalis* Reed. All preserved as internal moulds and all × 1.

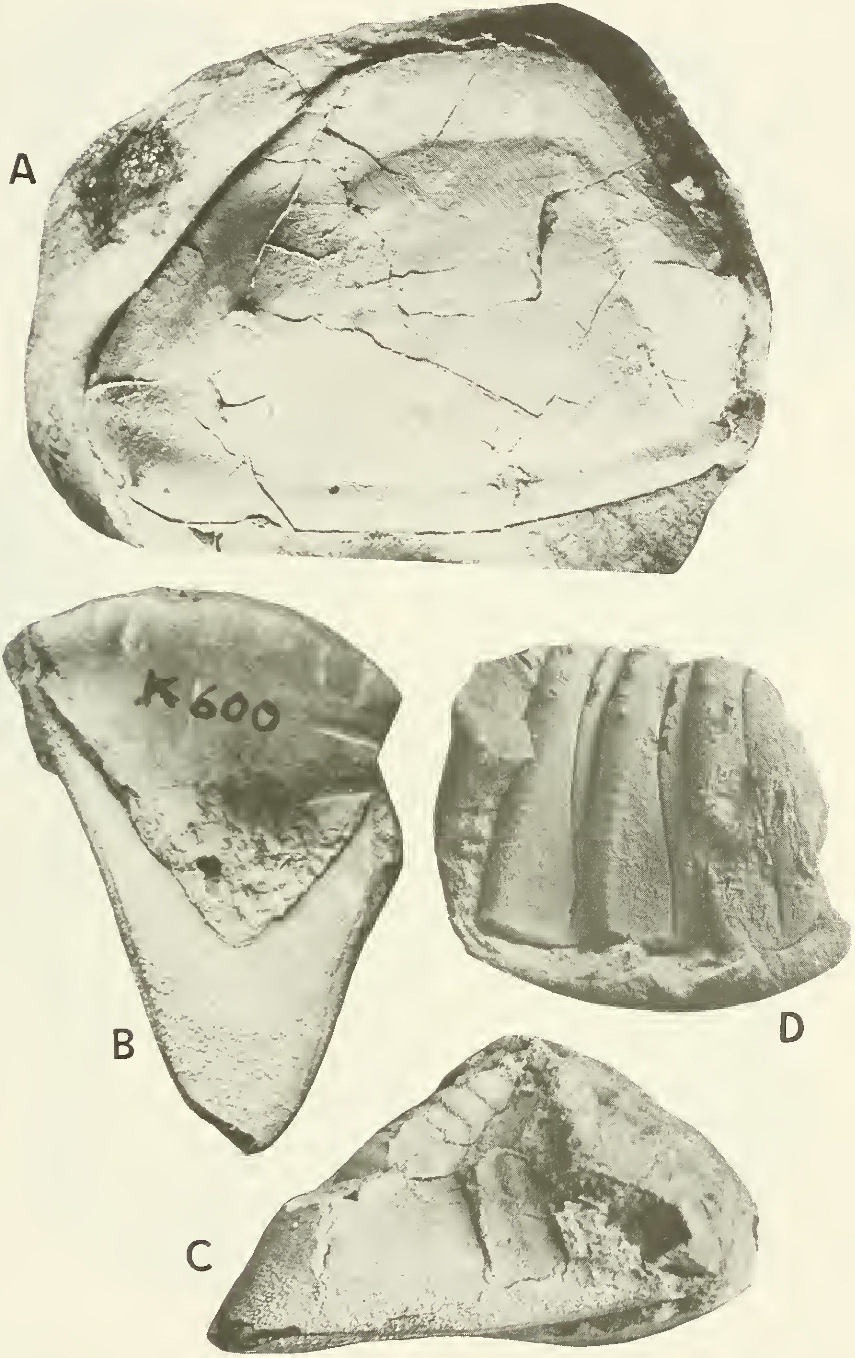

Fig. 17. *Burmeisteria herscheli* (Murchison). A. SAM–7199, the holotype of the var. *sodalis* Reed, figured by Reed (1925*a*, pl. 10 (fig. 5)), and preserved as an internal mould. B–C. SAM–PDB600, the original of Lake (1904, pl. 26, (fig. 3)), which retains cuticle. D. The lectotype, designated herein, of *Homalonotus lex* Schwarz, AM–1462, preserved as an internal mould, showing the distal terminations of the thoracic pleurae. All × 1.

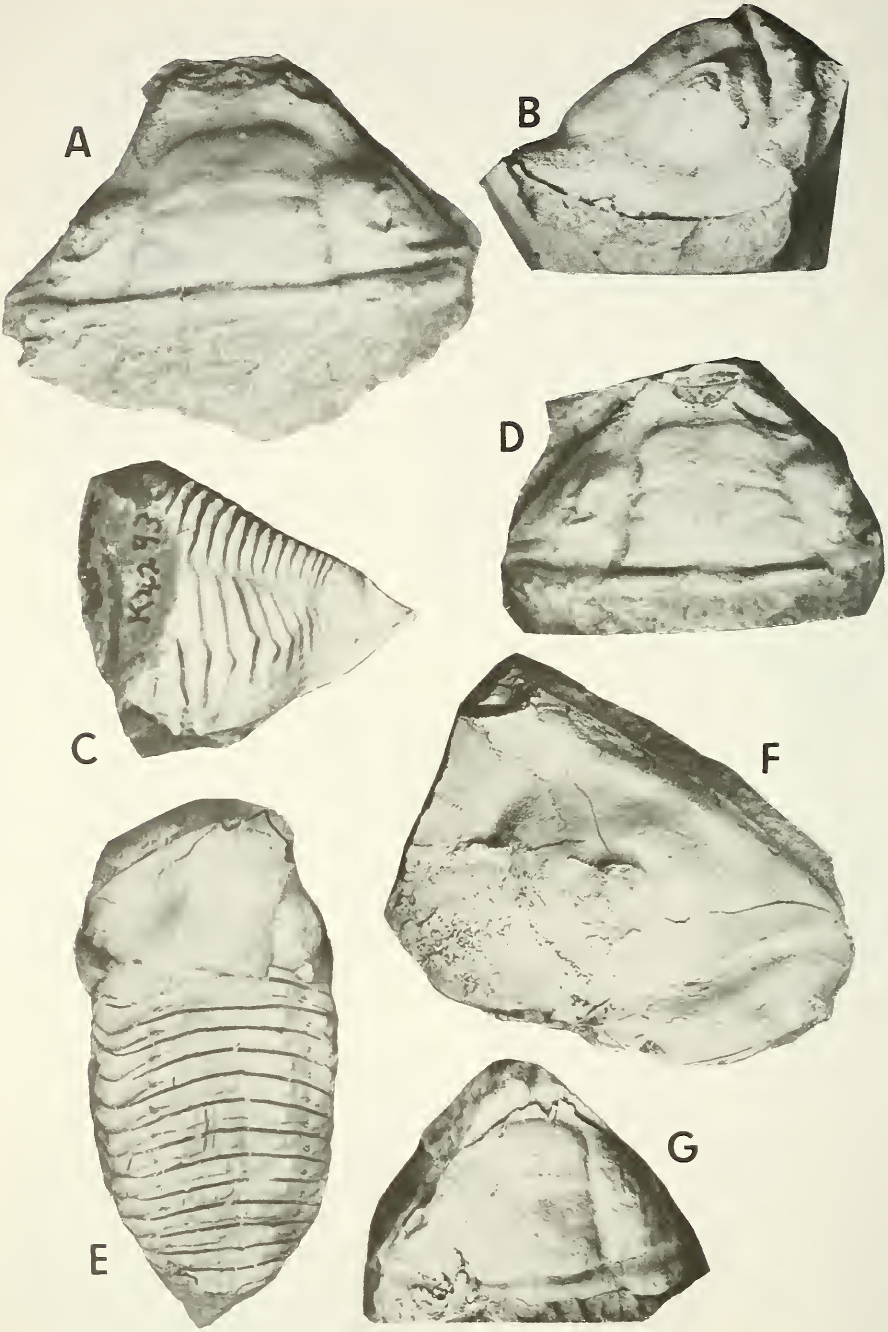

Fig. 18. *Burmeisteria herscheli* (Murchison). A–B. SAM–PDB4356. C. SAM–PDB4293. D. SAM–PDB4361, with a concave rostral suture. E. SAM–PDB4343. F. SAM–PDB4352. G. An unnumbered cephalon in the South African Museum. All preserved as internal moulds and all × 1.

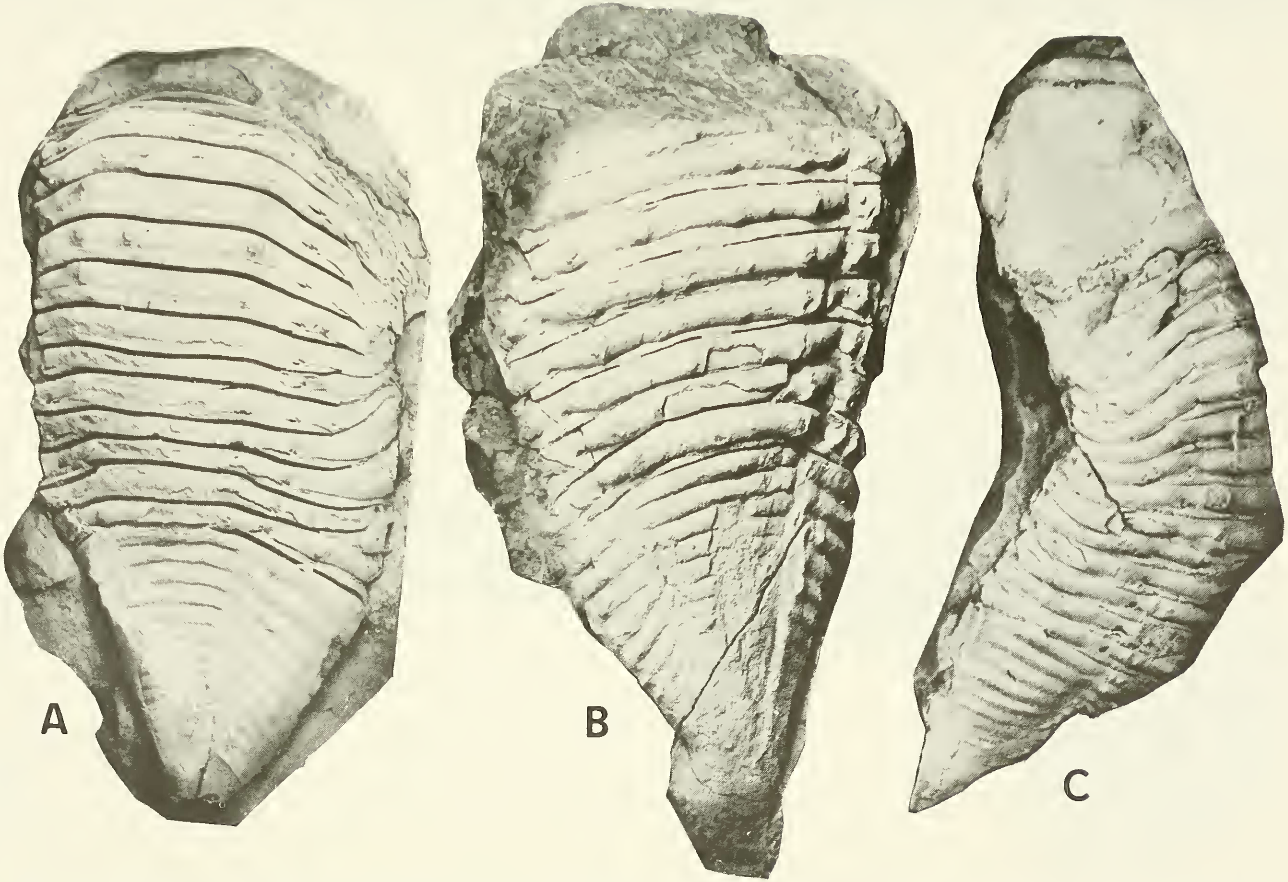

Fig. 19. *Burmeisteria herscheli* (Murchison). A. An unnumbered specimen in the South African Museum. B. SAM–PDB4364. C. SAM–PDB4359. All preserved as internal moulds and all × 1.

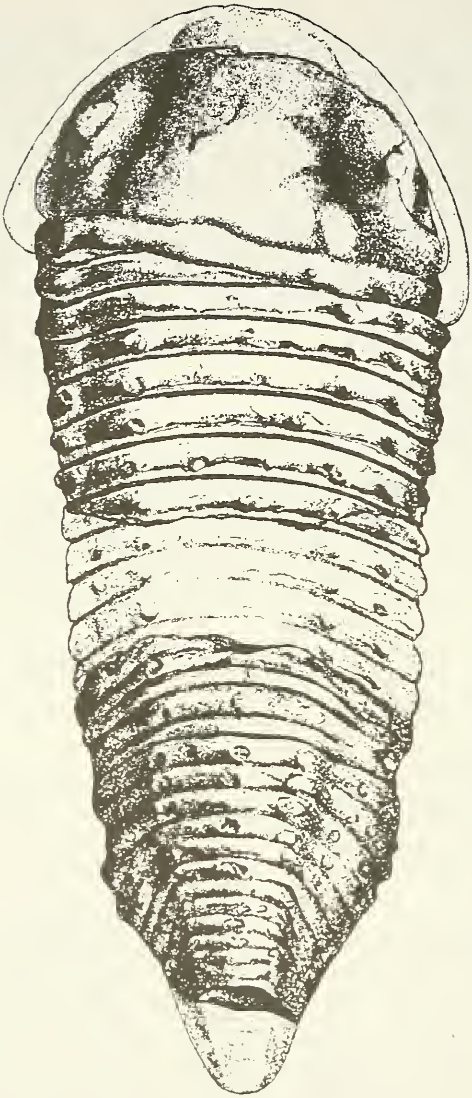

Fig. 20. *Burmeisteria herscheli* (Murchison).
The holotype, by monotypy, of *Homalonotus perarmatus* Frech,
almost certainly an internal mould (after Frech 1897). × 1.

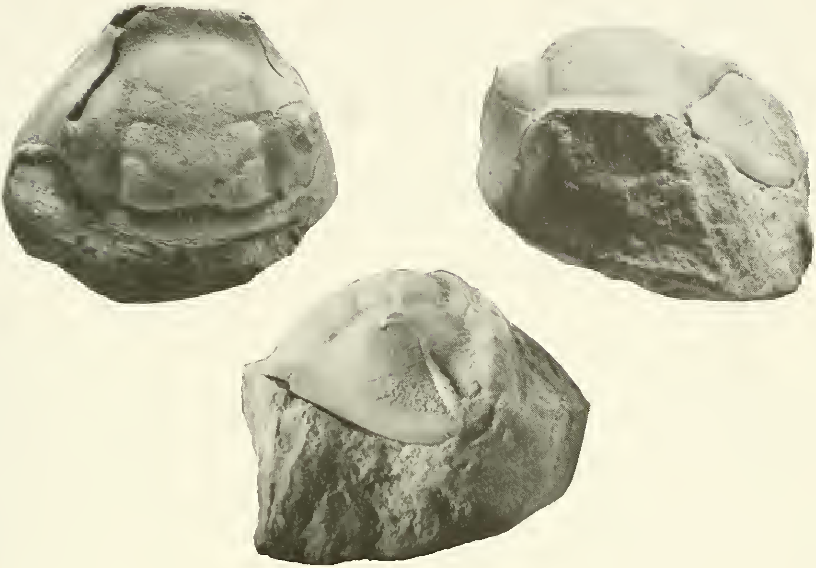

Fig. 21. *Burmeisteria herscheli* (Murchison). AM–2554, the original of Schwarz (1906, pl. 8 (fig. 8)), which was referred to the var. *grahami* Reed by Reed (1925*a*), preserved as an internal mould. × 1.

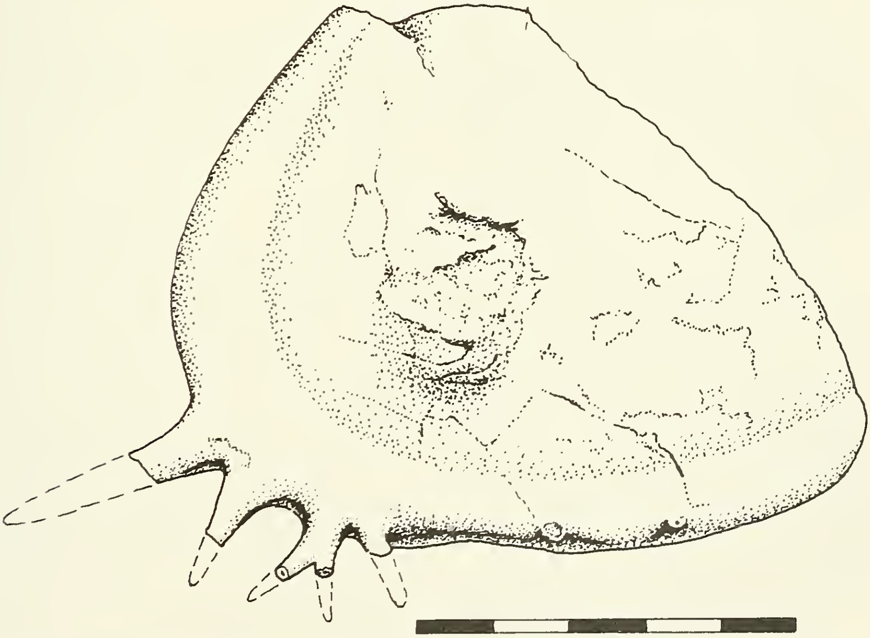

Fig. 22. *Burmeisteria herscheli* (Murchison). A genal fragment in the collection of R. Oosthuizen, showing the tubercles of the posterior border to represent spine bases, with some of the spines bifurcating. Scale = 5 cm.

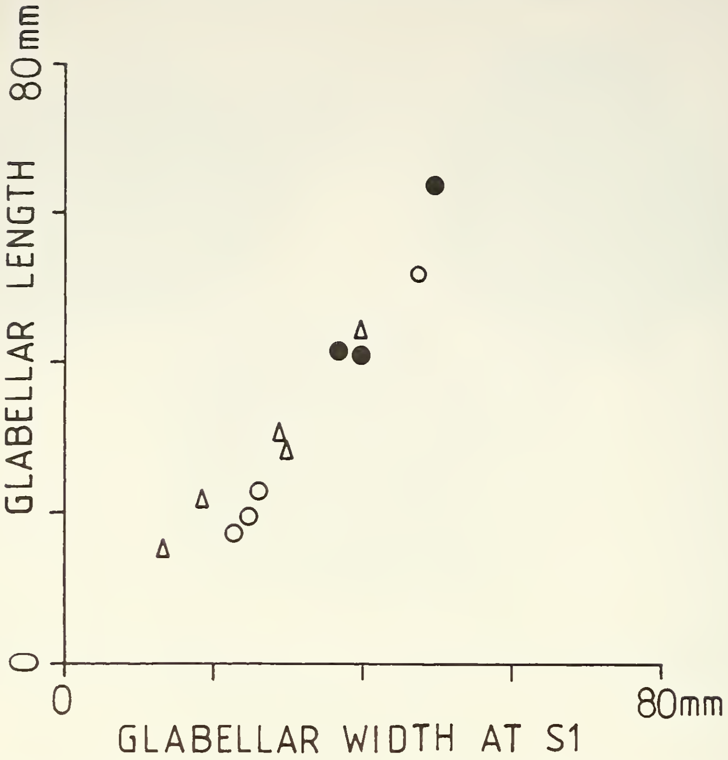

Fig. 23. *Burmeisteria herscheli* (Murchison). Plot of glabellar length (sag.) against glabellar width at the S1 sutures for the various rostral suture types. Circles = concave rostral suture; triangles = straight rostral sutures; dots = biconcave rostral sutures.

Discussion

This species is so similar to *B. herscheli* that it does not warrant additional description on the basis of the available material. The small cephalon that formed the basis of Reed's var. *africana* (Fig. 14C) shows the lack of tuberculation and relatively broad preglabellar field herein considered diagnostic of Clarke's species. It was assigned to *B. notica* by Reed (1925*a*: 185) ' . . . on account of its proportions, the truncate and emarginate anterior margin, the characters of the glabella, the course of the facial sutures, the well-rounded genal angles, and especially in the absence of tubercles and spine bases. But our specimen has a coarsely-granulated instead of smooth surface'. This latter feature is surely an artefact of preservation, the Bokkeveld example retaining cuticle, and hence Reed's varietal name is not used here.

The small individual (Fig. 30) referred by Reed (1925*a*: 168) to *B. herscheli* var. *rectisuturalis* shows the lack of tuberculation typical of *B. notica*, with the exception of a pair of spine bases on the posterior border just adaxial

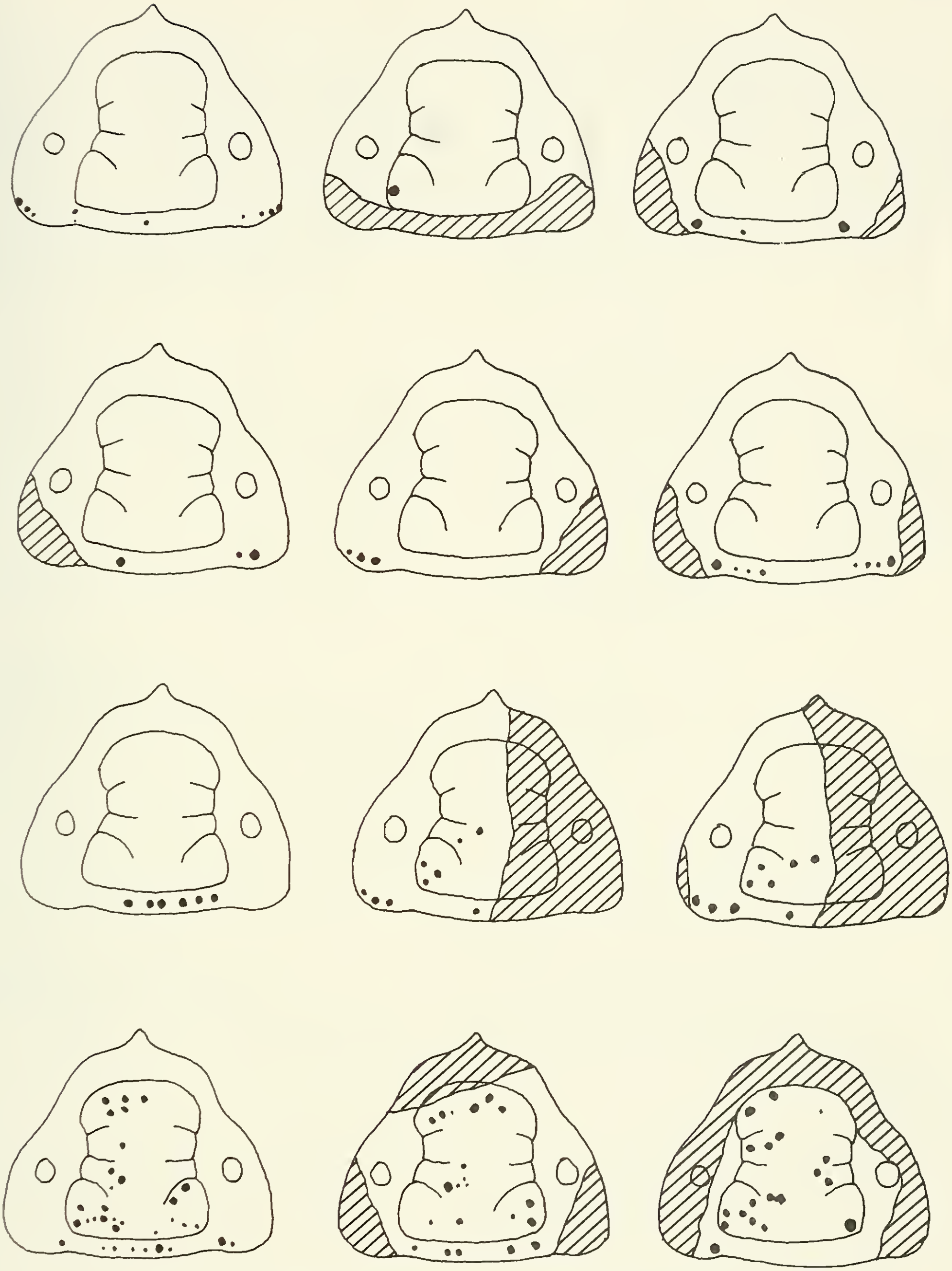

Fig. 24. *Burmeisteria herscheli* (Murchison).
Schematic representation of the cephalic tuberculation of various individuals.
Hatched areas not preserved.

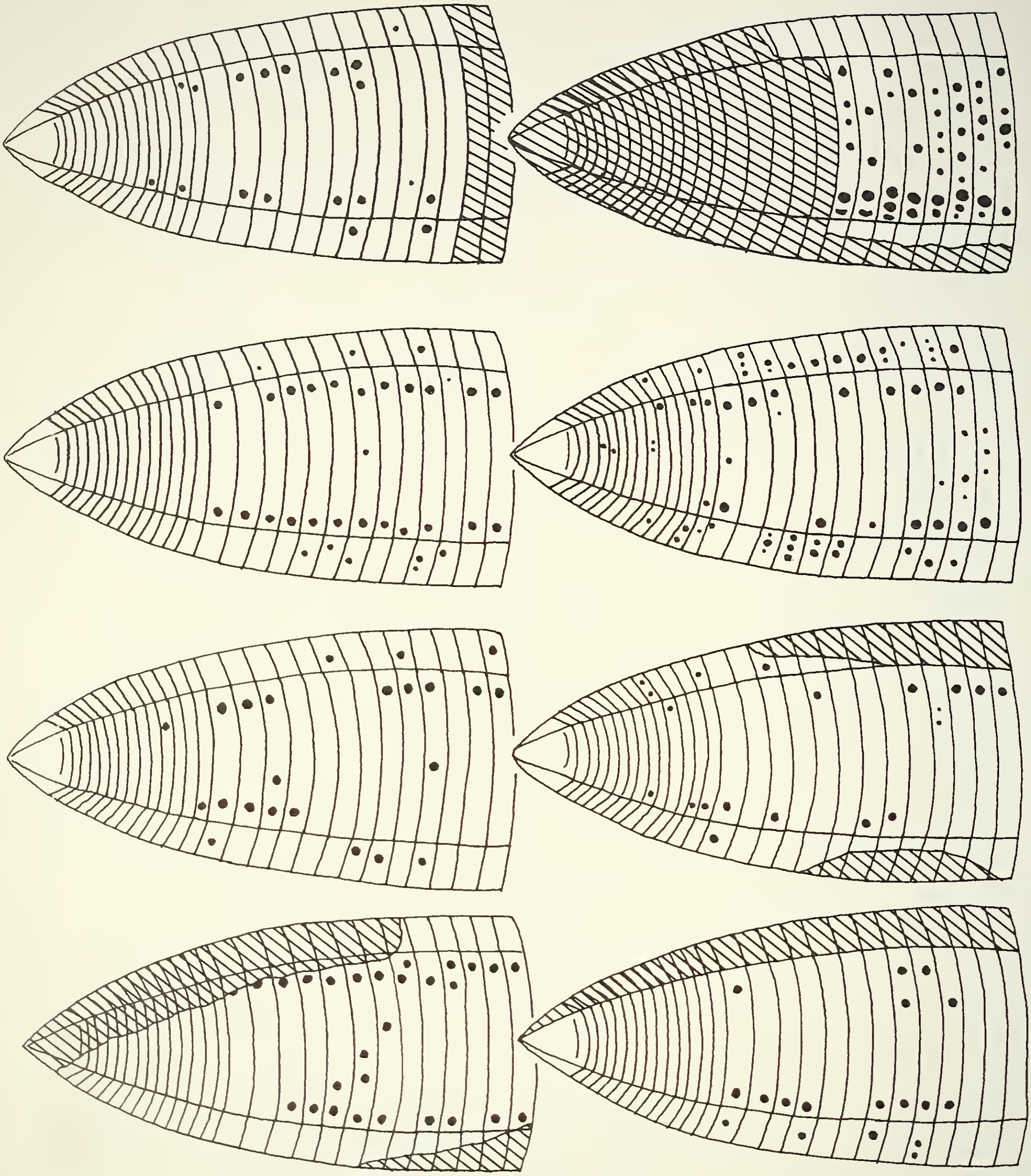

Fig. 25. *Burmeisteria herscheli* (Murchison).
Schematic representation of the thoracic and pygidial tuberculation of various individuals. Hatched areas not preserved.

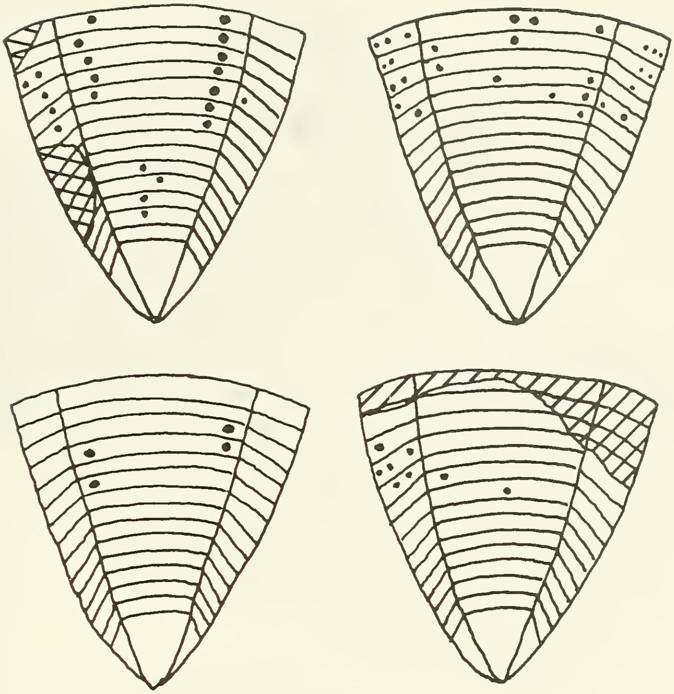

Fig. 26. *Burmeisteria herscheli* (Murchison).
Schematic representation of the pygidial tuberculation of
various individuals. Hatched areas not preserved.

of the genal angles. The importance of this feature is uncertain, since this individual also shows a pygidium with fewer axial rings (probably about 14) than *B. herscheli*, and hence also approaches *B. notica* in this respect.

Burmeisteria clarkei (Kozlowski) (1923: 24, pl. 1 (figs 12–15)) is very close to *B. notica* from which it was distinguished by the weaker trilobation and segmentation of the pygidium, with a slightly different outline, and in apparently having only 8 axial rings and 8 pairs of pleural ribs discernible. The differences are slight and objective population analysis is required to confirm the distinction of this species from *B. notica*.

Burmeisteria accraensis Saul (1967: 1129, pl. 143 (figs 1–8), pl. 144 (figs 1–16)) from the Devonian (Eifelian?) of Ghana was characterized by its lack of tuberculation and lobation, and especially by having the first ring furrow of the pygidium significantly deeper than the remainder. However, as noted by Saul (1967: 1134) this latter feature is also found in at least some individuals of *B. clarkei* while ' . . . the relative dimensions of *H. clarkei*, as measured from Kozlowski's plates, usually fall on the extreme peripheries of the scatter diagrams which exhibit the range of variation of the Accraian species'. Kozlowski's species, however, was said to have a more acuminate pygidium. Since the

Fig. 27. *Burmeisteria herscheli* var. *quernus* (Lake). A. SAM–626, the holotype of this variety and original of Lake (1904, pl. 27 (fig. 1)). B. The pygidial fragment figured by Lake (1904, pl. 27 (fig. 2)), in the South African Museum. Both preserved as internal moulds and both × 1.

Fig. 28. *Burmeisteria herscheli* var. *quernus* (Lake). A. SAM–2454, × 2. B. A specimen in the South African Museum, × 1,5. Both preserved as internal moulds.

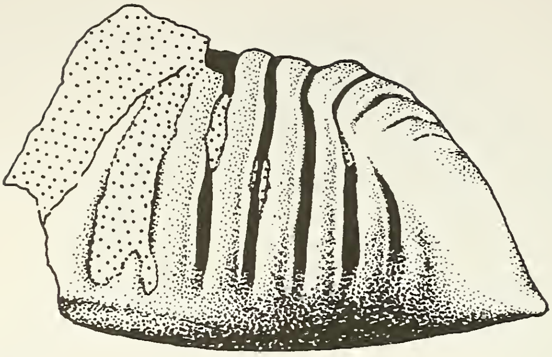

Fig. 29. *Burmeisteria antarctica* Saul.
A. 'Type I' pygidium in lateral view
(after Saul 1965). × 1.

Fig. 30. *Burmeisteria* cf. *notica* (Clarke). SU–C1, a juvenile preserved as an internal mould that may belong here. This specimen was referred to *Homalonotus herscheli* var. *rectisuturalis* by Reed (1925*a*). × 1.

population characteristics of *B. clarkei* are currently unknown, the differences between the two species are slight and questionably of specific importance. Saul (1967) failed to compare *B. accraensis* with *B. notica*. The lack of tuberculation and glabellar segmentation are all features of *B. notica* and in relative proportions the cephala of the two species are all but indistinguishable. Moreover, the pygidium of *B. notica* figured by Clarke (1913, pl. 2 (figs 11–12)) shows the same deep first ring furrow. *Burmeisteria accraensis* seems to differ from *B. notica* only in its slightly shorter (sag.) preglabellar field and slightly narrower pygidium, with all individuals apparently having the first ring furrow deepened.

'*Homalonotus*' *derbyi* Clarke (1890: 7, pl. 1 (figs 4, 7, 19)) was said to be '. . . an excellent representative of the subdivision *Trimerus*', while the lack of segmentation to the pleural areas of the pygidium of '*H*'. *kayseri* Thomas (1905: 245, pl. 11) suggests that it, too, may be a species of *Trimerus*.

Burmeisteria antarctica Saul was said to differ from *B. notica* in having a straighter and shorter rostral suture, a more indented posterior margin to the glabella, and a pygidium with deeper interpleural furrows becoming smooth near the posterior termination, and with a sharper break at the connection of ring furrows and rib furrows. Certainly 'Type I' pygidia are easily distinguished from *B. notica*, but the 'Type II' pygidia, which Saul (1965) failed to compare with *B. notica*, are very similar to Clarke's species. Clearly, however, the problem will be resolved only with the much-needed modern revision of Clarke's material.

Occurrence

Burmeisteria notica (Clarke) is currently recorded from Argentina, Bolivia, and the Bokkeveld succession. The definitely localized specimen in the collection of R. Oosthuizen comes from the Gydo Formation.

Burmeisteria fontinalis (Reed, 1925)

Fig. 31

Homalonotus (Digonus) fontinalis Reed, 1925*a*: 185, pl. 10 (fig. 6).

Material

Only the holotype, SMC–A3069, from Ezelfontein is currently known.

Description

Cephalon. The anterior portion of the cephalon is indistinct in the photograph of the holotype supplied by C. L. Forbes but, according to Reed (1925*a*: 185), it has a ' . . . truncate anterior edge, excavated in the middle'. The glabella is weakly inflated, almost flat, and with indistinct lobation. It is subrectangular in outline, narrowing slightly to the anterior. The glabellar

Fig. 31. *Burmeisteria fontinalis* (Reed). The holotype, by monotypy, SMC–A3069, presumably an internal mould. Note the lack of tuberculation and numerous pleurae to the pygidium. Approx. ×5.

furrows are all directed strongly posteromedially and all seem to be slightly convex anteromedially. The occipital furrow is straight, narrow, of uniform depth and distinctly narrower than the occipital ring. The posterior border furrows are distinct and the posterior borders broaden (exsag.) abaxially. The cheeks are poorly preserved but there appear to be weakly developed paraglabellar areas, and the small eyes are raised on prominent bosses. The surface of the cephalon is granulose but discrete tubercles are lacking.

Thorax. The thorax is poorly preserved, but with a wide axis, 13 segments and a granulose surface.

Pygidium. The pygidium is strongly convex, subtrigonal in outline and with well-developed trilobation. The axis is rather broad anteriorly and tapers posteriorly into a bluntly rounded tip to leave a short post-axial field. The axis comprises about 15 rings which are slightly wider than the ring furrows. The pleural fields are subtrigonal and ornamented with 14–15 sharply raised, distinct ribs which reach the pygidial margin and are said to be ornamented with coarse granules.

Discussion

This species is most closely related to *B. notica* (Clarke) and its allies. It differs from *B. notica* by its shorter preglabellar area, its relatively much longer glabella, and especially in the characters of the pygidium, *B. fontinalis* having many more pleural ribs than Clarke's species. The above differences also serve to distinguish *B. fontinalis* from *B. clarkei* (Kozlowski) and *B. accraensis* Saul.

Occurrence

Burmeisteria fontinalis (Reed) is known only by the holotype which comes from an unknown level in the Bokkeveld sequence.

Superfamily DALMANITACEA Vogdes, 1890

Family **Dalmanitidae** Vogdes, 1890

Subfamily Dalmanitinae Vogdes, 1890

Genus *Francovichia* Braniša & Vaněk, 1973

Type species *Odontochile branisi* Wolfart, 1968;
by original designation

Francovichia clarkei (Ulrich, 1893)

Figs 32A, 33D, 34A, 35–36, 37A–B

Dalmanites clarkei Ulrich, 1893: 19, pl. 1 (fig. 13). Lake, 1906: 429. Knod, 1908: 500. Kozlowski, 1923: 106. Swartz, 1925: 34.
Dalmanites lunatus Lake, 1904: 212, pl. 25 (fig. 6).
Dalmanites sp., Lake, 1904: 212, pl. 25 (fig. 7).
Non Dalmanites lunatus Lambert, 1904: 482, pl. 44 (figs 1–3, 5) (= *D. limurulus* (Green) *fide* Delo, 1940).
Dalmanites (Hausmannia) dunni Reed, 1925*a*: 133, pl. 11 (fig. 5).
Dalmanites (Hausmannia) lunatus Lake, Reed, 1925*a*: 135.
Phacops sp., Brink, 1951: 162, figs 1–2.
Odontochile clarkei (Ulrich) Wolfart, 1968: 75.

Material

The holotypes of *Dalmanites lunatus* Lake, SAM–66, and *D. dunni* Reed, SAM–3949, together with RO–5, 51, 780, 783, PRV–34–35, 623, and BPI–i113 and i243.

Description

Cephalon. The cephalon is known, among South African material, largely from the holotype of *D. lunatus* Lake (Fig. 35). This shows it to have been semicircular, transversely much wider than long (sag.), and with prominent genal spines extending backwards as far as the fourth thoracic segment. The

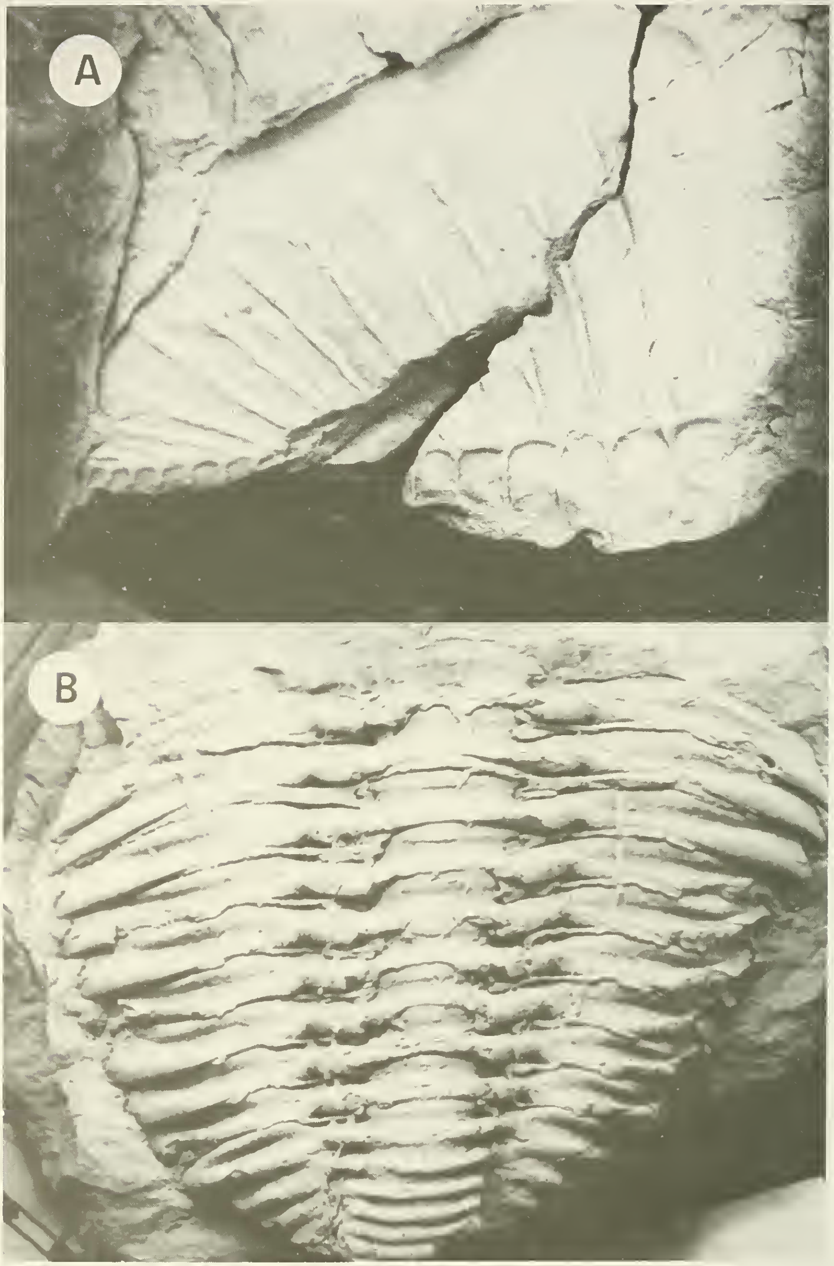

Fig. 32. A. *Francovichia clarkei* (Ulrich). The holotype, by monotypy, of *Dalmanites (Hausmannia) dunni* Reed (1925*a*, pl. 11 (fig. 5)), in the South African Museum, SAM–3949, preserved as an external mould. B. Gen. et sp. indet. SAM–784, the original of Lake (1904, pl. 25 (fig. 5)), preserved as an internal mould. Both × 1.5.

glabella expands anteriorly, with a much enlarged frontal lobe, but the anterior region of the cephalon is too poorly preserved to be certain of the characters in this region. The 3p furrows are fairly deep and directed strongly posteromedially. The 2p and 1p furrows are moderately deep, transverse, and seem to connect with the well-developed axial furrows. Both the L1 and L2 lobes are of more or less constant width (exsag.). The occipital furrow is transverse, and the smooth occipital ring seems to be broadest sagittally. The posterior border furrows are deep and transverse, whereas the lateral border furrows are shallow. The eye is very large, certainly 50 per cent of the exsaggital cephalic length. A well-preserved eye that seems to belong to this species (Fig. 36) comprises about 50 vertical files of lenses, with 15 ocelli in the central file and a total of about 577 ocelli to the visual surface. It also shows an unornamented palpebral lobe weakly separated from the unornamented palpebral area, as well as a shallow subocular groove separating the eye from the socle. The posterior branch of the facial suture curves strongly forward before recurving to meet the lateral border well in front of the posterior margin to the eye.

Thorax. The thorax comprises 11 segments, with a rather low, weakly convex axis about one-third of the thoracic width. The ring furrows are very much narrower than the axial rings themselves. The axis broadens (trans.) to the third or fourth ring whereafter it tapers slowly to the posterior. The pleural grooves are pronounced, with finer, narrower interpleural furrows.

Pygidium. Although the pygidium of *D. lunatus* is poorly preserved, *Dalmanites dunni* is based upon adult topotype material (Fig. 32A) and, together with additional topotype material, allows for a relatively comprehensive description of the pygidium of this species.

The pygidium is large, triangular, distinctly wider (trans.) than long (sag.), and with a long, narrow axis. The axis tapers regularly to the posterior, and comprises 18–21 rings. After the tenth axial ring, the ring furrows become obsolete sagittally. In none of the available material is the terminal portion of the pygidium preserved, but in BPI–i243 (Fig. 37A–B) it is at least distinctly mucronate; it is assumed to have had a terminal spine as in the South American material. The pleural fields are broad, subtrigonal, strongly downturned at the margins in well-preserved material, and with an entire border. There are 11 pairs of well-developed, flat-topped ribs, each bearing a very faint interpleural furrow and separated by a deep, but narrow (exsag.) pleural groove, with a very reduced and indistinct twelfth pair to the posterior. In the anterior pleurae, the pleural grooves meet the axis almost at right angles, but the angle becomes increasingly acute to the posterior, until the final few ribs are almost parallel to the axis. The pleural segmentation is effaced distally to leave a smooth narrow border. BPI–i243 retains granulose cuticle.

Discussion

Both Lake (1904) and Reed (1925*a*) remarked on the close similarity between *D. dunni* and *D. clarkei* without effectively distinguishing them. The

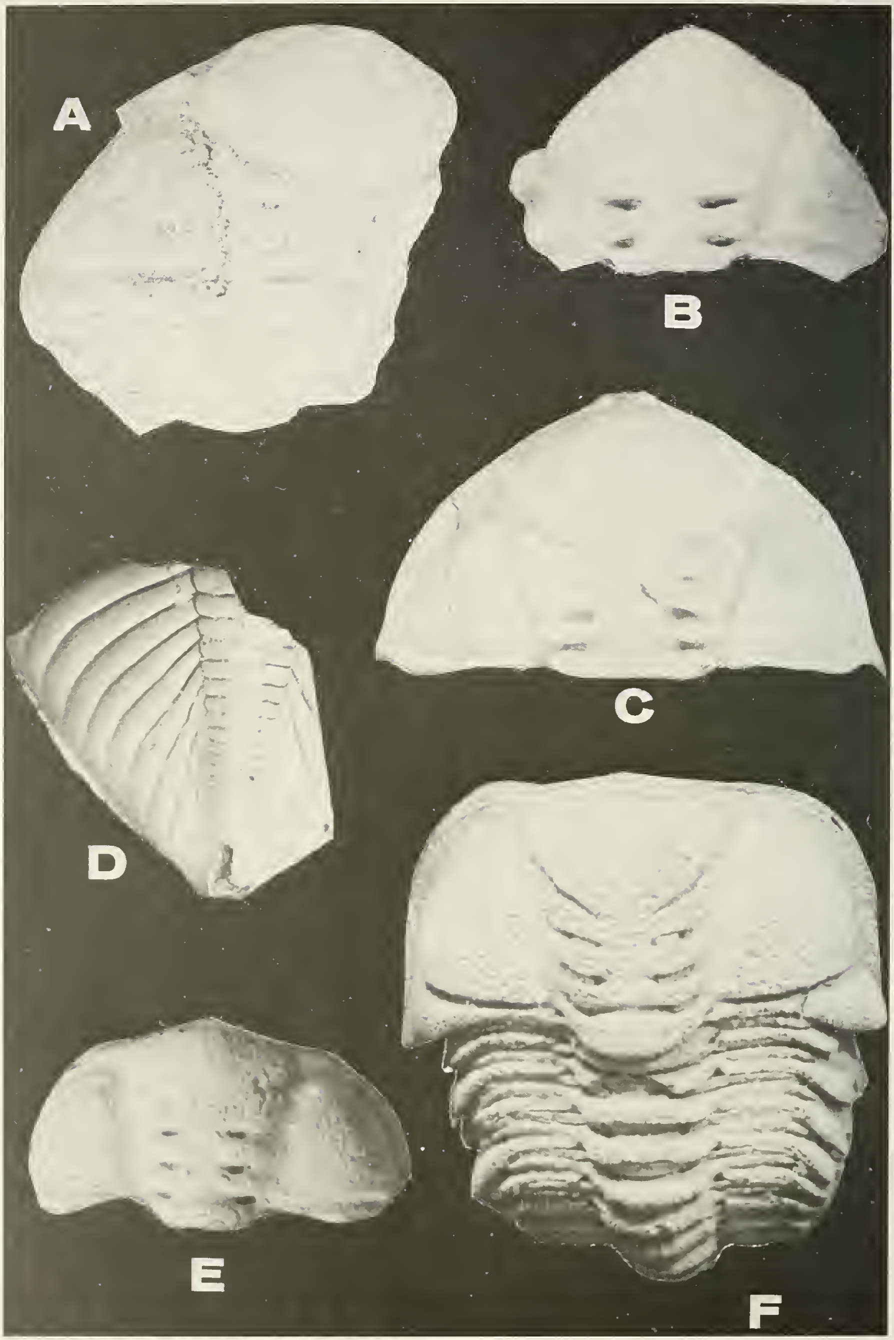

Fig. 33. A, C. *Metacryphaeus caffer* (Salter). A. SU–H76, the holotype of *Eocorycephalus capensis* (Reed) (1925*a*, pl. 8 (fig. 5)). C. SU–C2, the holotype of *Dalmanites (Proboloides) ensifer* Reed (1925*a*, pl. 8 (fig. 4)), which probably belongs to Salter's species. Compare with Figure 39F. × 1.5. B. *Bainella africana* (Salter). SU–K461. × 1. D. *Francovichia clarkei* (Ulrich). RO–5. × 1. E–F. *Typhloniscus baini* Salter. E. RO–702: note the 'eye ridges'. × 1. F. RO–753, an individual retaining cuticle. × 2.

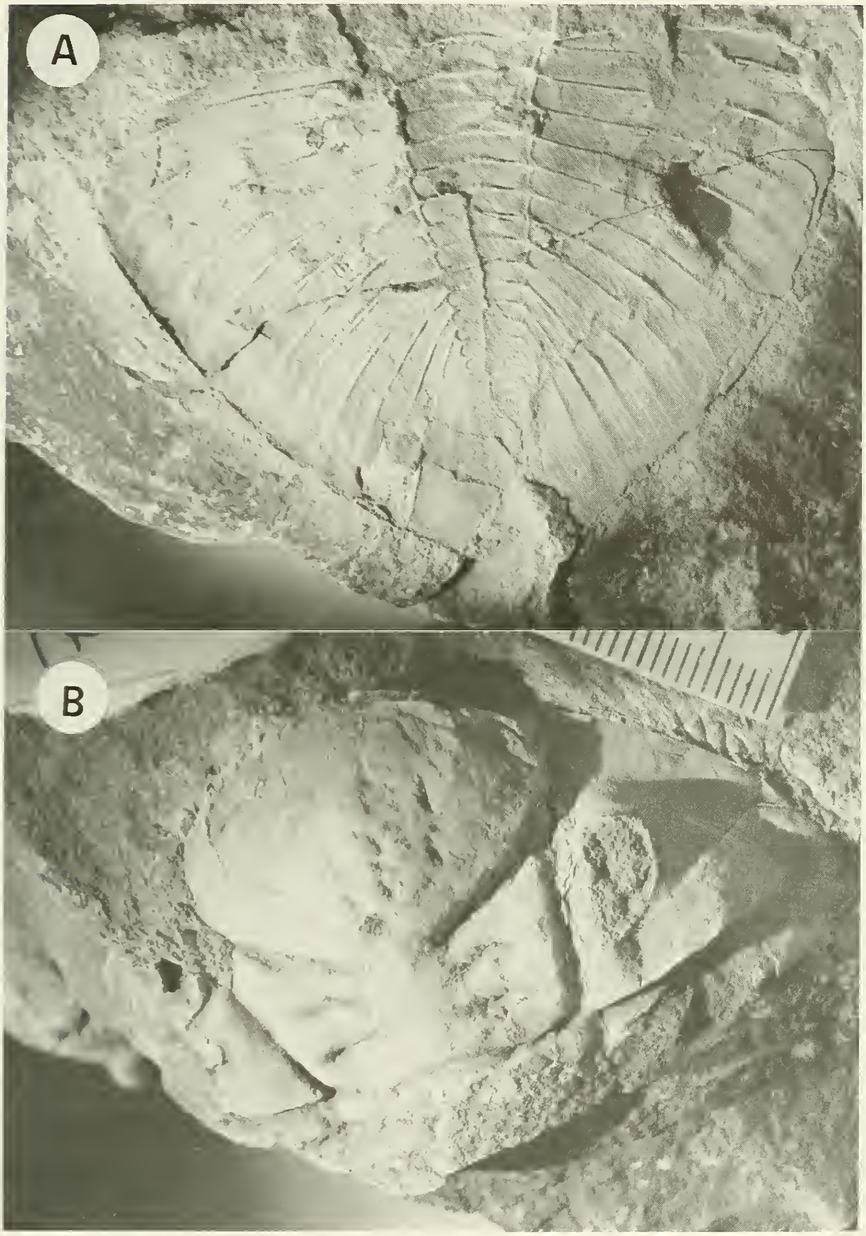

Fig. 34. A. *Francovichia clarkei* (Ulrich). PRV–623, an external mould. × 1,3. B. *Metacryphaeus caffer* (Salter). PRV–1028, an internal mould showing a prominent auxiliary impression system. × 1,8.

Fig. 35. *Francovichia clarkei* (Ulrich). Plasticine squeeze of the holotype of *Dalmanites lunatus* Lake (1904, pl. 25 (fig. 6)), an external mould. Note the very large eyes. ×5.

writer cannot find any significant characters to separate these two species, and *D. dunni* is considered a junior subjective synonym of *Francovichia clarkei*.

Dalmanites lunatus Lake is based upon an incomplete juvenile (Fig. 35) that was collected from the same locality (Gamkapoort) as the holotype and topotype material of *D. dunni*. As such, the two species seem to be based upon different parts of different ontogenetic stages of the same animal and they are herein regarded as conspecific. *Dalmanites lunatus* Lake is, therefore, included in the synonymy of Ulrich's species.

In the same year that Lake (1904) created his species, Lambert (1904) also described a new species as *Dalmanites lunatus* from the Silurian of North America. Since, according to Delo (1940: 44), *D. lunatus* Lambert (*non* Lake) is a synonym of *D. limurulus* (Green), while Lake's homonym is here included in the synonymy of *F. clarkei*, this is a case for letting sleeping dogs lie and the nomenclatural priorities of these two names are ignored.

Francovichia branisi (Wolfart) (1968: 72, pl. 6 (fig. 3), pl. 7 (figs 1–2)) is very close to the present species. According to Wolfart (1968), there are 20–22 axial rings and 14 pairs of pleural ribs to the pygidium of *F. branisi*, which was also said to have a somewhat narrower pygidium (with margins that are weakly concave posteriorly) than *F. clarkei*. The differences in outline and width are slight and may reflect merely intraspecific variation. Moreover, it is difficult to determine more than 17 axial rings on the pygidium of *F. branisi* figured by Wolfart (1968, pl. 6 (fig. 3)), or more than 12 pairs of pleural ribs. *Francovichia branisi* does, however, seem to have smaller eyes and is for the present retained as distinct.

'*Dalmanites*' *andii* Kozlowski (1923: 38, pl. 2 (figs 3–4)) differs from the present species in having a much wider pygidium, and with prominent interpleural furrows that are almost as wide as the ribs. These are also much the same characters that distinguish '*Dalmanites*' *patacamayaensis* Kozlowski (1923: 36, pl. 2 (fig. 2)), *Odontochile dunbari* Delo (1940: 56, pl. 5 (fig. 7)) and *O. micrurus* (Green) (Delo, 1940: 58, pl. 5 (figs 1–2)). The '*Dalmanites*' *maecurua* Clarke figured by Knod (1908: 500, pl. 21 (fig. 3)) seems to have fewer axial rings and wider interpleural grooves, which extend to the pygidial margin, than the present species.

Occurrence

Francovichia clarkei (Ulrich) is currently known only from the Icla Formation of Bolivia and the Gydo Formation of the Bokkeveld sequence.

Family **Synphoriidae** Delo, 1935

Discussion

The evolution and phylogeny of this largely North American family has been discussed at length by Lespérance & Bourque (1971, 1973) and Lespérance (1975), and two subfamilies are currently recognized, the Synphoriinae

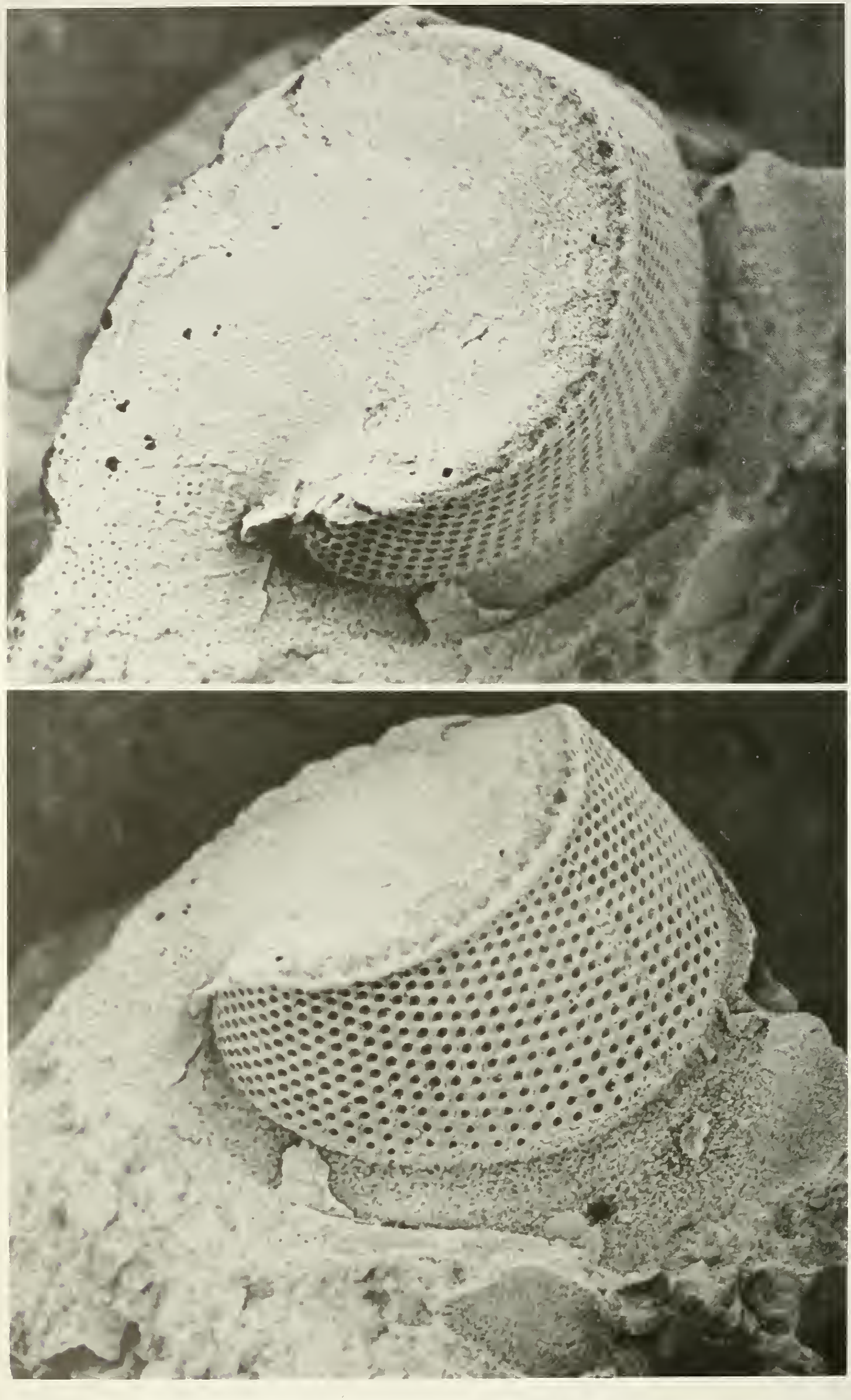

Fig. 36. *Franchovichia clarkei* (Ulrich). BPI–i113. The large eye figured by Brink (1951, figs 1–2), preserved as an internal mould. × 2.5.

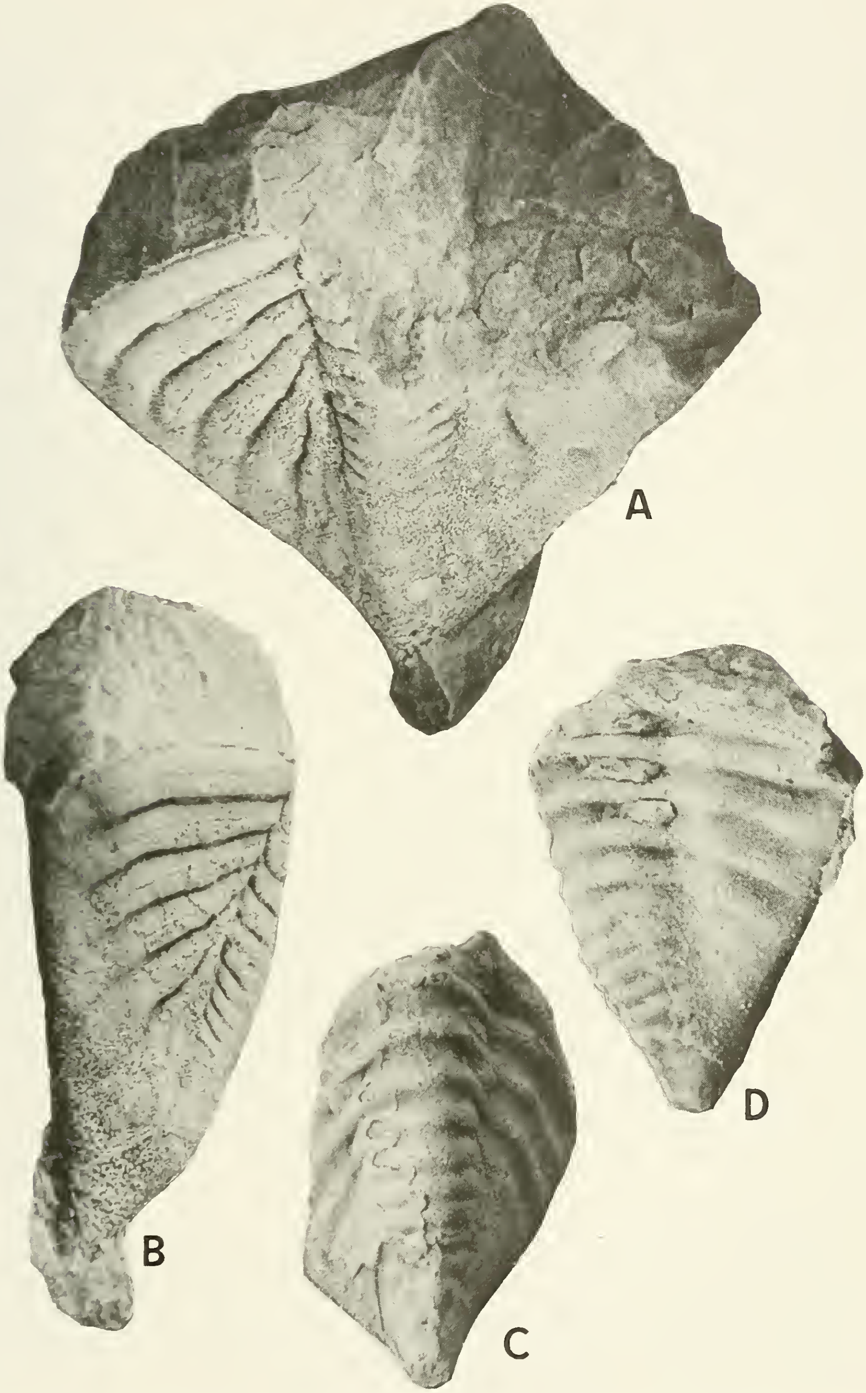

Fig. 37. A–B. *Francovichia clarkei* (Ulrich). BPI–i243, which seems to retain cuticle. × 2,4. C–D. *Bainella* sp. nov. BPI–i244, a pygidium retaining cuticle. Note the weak tubercles on the ribs at the pleural axis. × 2.

and Trypaulitinae, with the origins of the family lying in '. . . a generalized Silurian *Odontochile*' (Lespérance 1975: 99). Braniša & Vaněk (1973) introduced three new genera from the Devonian of Bolivia that they believed should be included here; these were *Gamonedaspis*, *Fenestraspis*, and *Chacomurus*. However, only *Chacomurus* was accepted as a true representative of the Synphoriidae by Lespérance (1975), who included it in the subfamily Trypaulitinae. Both *Gamonedaspis* and *Fenestraspis* were excluded because '. . . they do not possess the characteristics of the family as now understood' (Lespérance 1975: 101). It is perhaps significant, however, that Lespérance & Bourque (1971) provisionally included *Dalmanites accola* Clarke in the Synphoriinae, although Lespérance (1975: 103) later concluded that '. . . no compelling evidence exists for [its] inclusion in the Synphoriidae'. Contrary to the opinion of Lespérance (1975), however, *Dalmanites boehmi* Knod and the perhaps conspecific *D. accola* Clarke are very close to certain Synphoriidae, especially *Roncellia* and *Anchiopsis*. The Malvinokaffric species, on the face of it, seem to be very closely related to *Roncellia perceensis* (Clarke) (Delo 1940: 59, pl. 5 (figs 5–6), pl. 6 (fig. 7); Lespérance & Bourque 1971: 190, pl. 26 (figs 1–3)), the main points of difference being the relatively narrower pygidium with fewer pleural ribs of the Malvinokaffric species. Since these differences are no greater than those between many species of dalmanitid trilobites, one is left wondering whether the Malvinokaffric species should not be included in the genus *Roncellia*. However, *Dalmanites boehmi* and *D. accola* both differ from typical *Roncellia* in having a median tubercle to the occipital spine, in which respect they approach *Anchiopsis*. The pygidium of the latter genus is sufficiently distinct, however, to preclude reference of the Malvinokaffric species to this taxon.

The type species of *Gamonedaspis*, *G. scutata* Braniša & Vaněk (1973: 98, pl. 1 (fig. 6), pl. 4 (figs 1–2)), is known only from pygidia that show the following features: longer than wide, subtrigonal in outline, and terminating in an uptilted postaxial spine. The axis tapers rather rapidly to the posterior and comprises 13–14 rings, whereafter the segmentation becomes indistinct. There are 9–10 pairs of pleural ribs, of which the anterior 3–4 show faint pleural grooves. There are two longitudinal rows of tubercles on the axis and randomly scattered tubercles on the pleural ribs. Thus, *G. scutata* differs from *Dalmanites boehmi* and *D. accola* mainly in its uptilted post-axial spine. On the basis of available evidence the differences are not herein considered of generic importance and the writer would also refer *D. boehmi* Knod, *D. boehmi* var. *boliviensis* Kozlowski, and *D. accola* to the genus *Gamonedaspis*.

Whether the resemblances between *Gamonedaspis* and *Roncellia* are another example of the perturbing homoeomorphy between boreal and Malvinokaffric trilobites is at present uncertain. On the face of it, *Roncellia*, *Anchiopsis*, *Dalmanitoides*, and *Gamonedaspis* show sufficient similarities to suggest they may form a third lineage within the Synphoriidae.

Subfamily Synphoriinae Delo, 1935

Genus *Gamonedaspis* Braniša & Vaněk, 1973

Type species *Gamonedaspis scutata* Braniša & Vaněk, 1973;
by original designation

Gamonedaspis boehmi (Knod, 1908)

Figs 7A, 38, 39D, 40, 41A, 42C, 43, 44A

Dalmanites böhmi Knod, 1908: 568, pl. 21 (fig. 1)
Dalmanites boehmi var. *boliviensis* Kozlowski, 1923: 36, pl. 2 (fig. 1). Swartz, 1925: 34. Wolfart 1968: 70.
Dalmanites boehmi (Knod) Reed, 1925*a*: 133.
Francovichia? boehmi (Knod) Eldredge & Ormiston, 1979: 162.

Material

Thirteen specimens, SAM–PDB3997, 4056, 4070, 4332, 4336, 4338–4339, 4348, 4358, RO–282, and PRV–34, 126, 1096, all preserved as internal moulds.

Description

Cephalon. The cephalon is semicircular in outline, about twice as wide as the sagittal length, and weakly convex. The genal angles are not preserved in the South African material but are assumed to be as in Knod's (1908) figured type. The axial furrows are strongly impressed and diverge markedly to the anterior. There is a narrow preglabellar field that forms a bluntly rounded median rostrum (Fig. 41A). The 3p furrows are rather deep, directed strongly

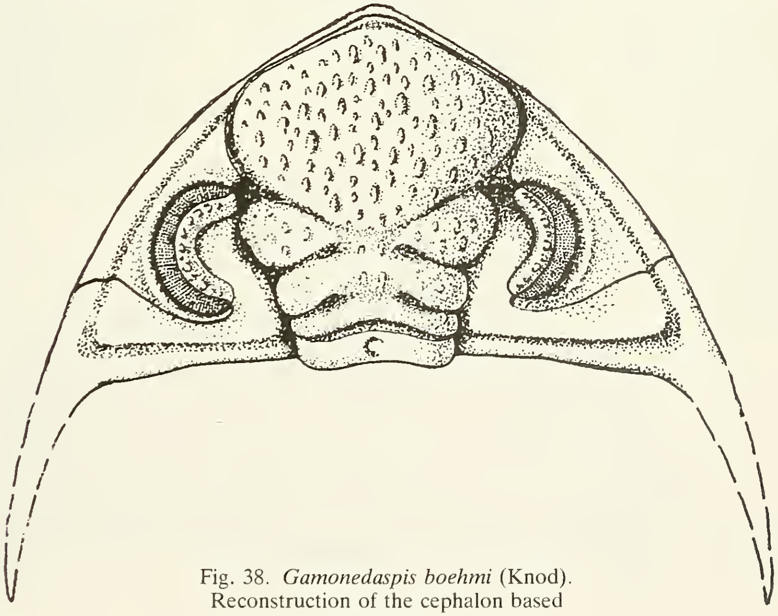

Fig. 38. *Gamonedaspis boehmi* (Knod). Reconstruction of the cephalon based upon the available material. × 1.

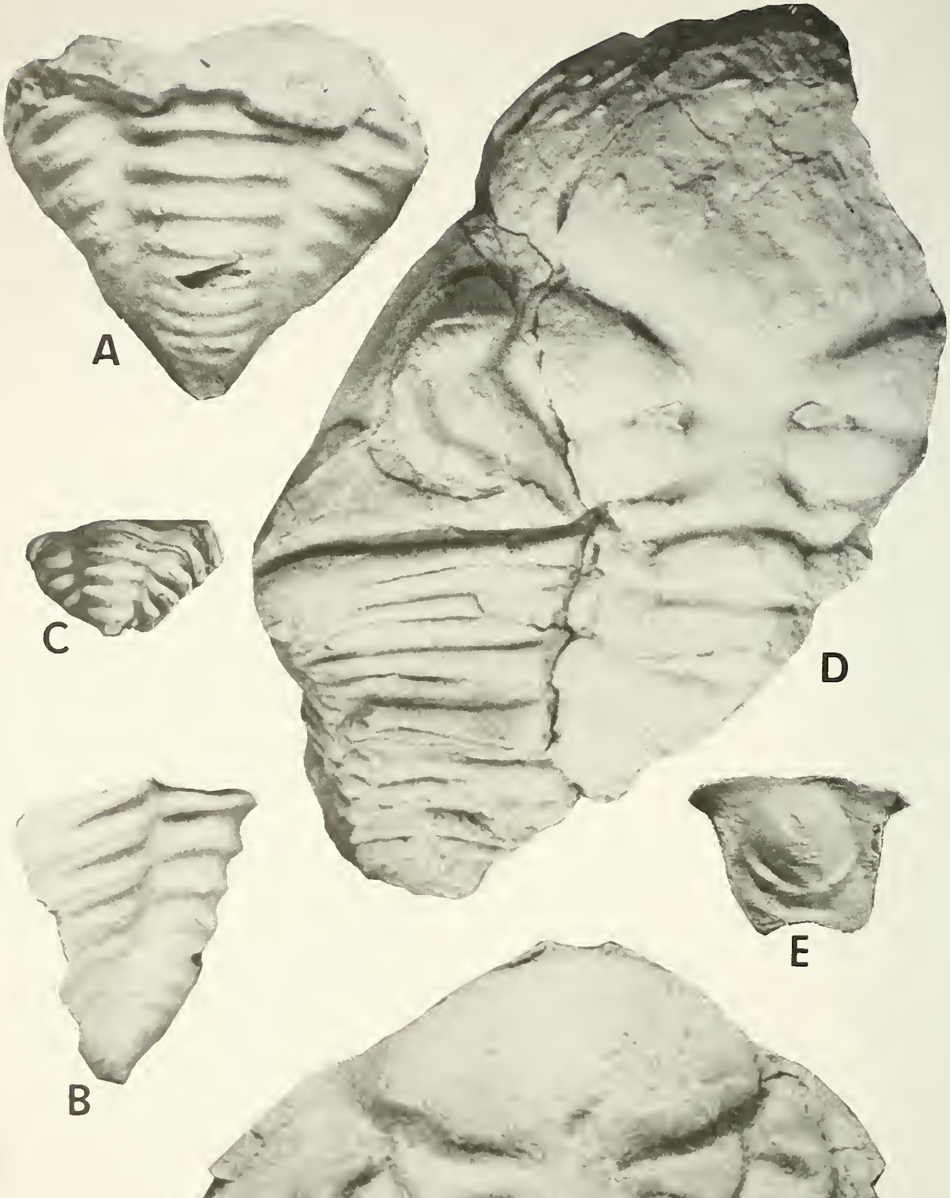

Fig. 39. A–B. *Bainella africana* (Salter). SAM–PDB3076. × 2. C. *Typhloniscus baini* Salter. RO–702a, a pygidium. × 1.1. D. *Gamonedaspis boehmi* (Knod). SAM–PDB4338. × 2. E. *Burmeisteria herscheli* (Murchison). An hypostoma. RO–279. × 1. F. *Metacryphaeus caffer* (Salter). SAM–3960. × 2. All specimens preserved as internal moulds.

posteromedially, and almost meet adaxially. They are weakly connected proximally by a shallow transglabellar furrow that serves to isolate the prominent, coarsely tuberculate, rhomboidal frontal lobe. The 2p and 1p furrows are moderately deep, subparallel, with prominent adaxial apodemal pits, and distinctly joined to the axial furrows. In large individuals (Fig. 39D), the L3 lobes protrude laterally almost as much as the frontal lobe, while the L1 lobes are very narrow (exsag.) and reduced. In PRV–126a (Fig. 7A), the 3p and 2p furrows are joined proximally, so as to isolate the L3 lobes, while the 2p and 1p furrows are also weakly joined, tending to isolate the L2 lobes. Moreover, the 2p and 1p furrows are weakly connected across the glabella (Fig. 43A) by variably developed transglabellar furrows. The occipital furrow is rather narrow, with apodemal pits distally, and separates the moderately broad occipital ring that bears a prominent median tubercle (spine base?). The cheeks are subtrigonal in outline, moderately downturned, with very deep posterior border furrows and posterior borders which broaden (exsag.) abaxially. There are distinct palpebral furrows that connect with the axial furrows anteriorly and, seemingly, with the furrow separating the eye from its socle posteriorly. The cheeks lack tuberculation, although there are small tubercles on the palpebral lobes above the eyes. The eyes are large, arcuate, about half the exsagittal length of the cephalon, and separated from the L3 lobes anteriorly only by the axial furrows. The visual surface comprises about 30–32 subvertical rows of ocelli, with 8–9 lenses in the central files. The anterior ramus of the facial suture touches, but does not transect, the lateral margin of the frontal lobe. The posterior branch curves strongly forward before recurving sharply to meet the lateral border in front of the posterior margin of the eye.

Thorax. Poorly known from South African material. So far as can be ascertained there are no median tubercles to the axis nor any tubercles on the pleurae. The axial furrows are moderately impressed, and there are deep pleural grooves to the pleurae, which are separated by distinct interpleural furrows. The distal terminations of the pleurae are unknown.

Pygidium. The pygidium is triangular, slightly wider than the sagittal length (if the length of the post-axial spine is excluded), with gently convex borders and a short terminal spine. The axis tapers uniformly to the posterior and comprises between 15–18 rings, the segmentation becoming indistinct posteriorly, each ornamented with a pair of tubercles close to the sagittal line. The pleural fields are subtrigonal and separated from the axis by prominent axial furrows. There are 11 pairs of rather broad, flat-topped ribs, the anterior 6–7 with faint pleural grooves. The interpleural furrows are deep and clearly defined, and much narrower than the ribs. The pleural ribs meet the axis at an acute angle (almost at right angles for the first few pleurae), which increases to the posterior. A few randomly scattered tubercles of varying sizes ornament the pleural fields, some situated directly upon the faint pleural grooves, and show a tendency to mark the fulcral axis.

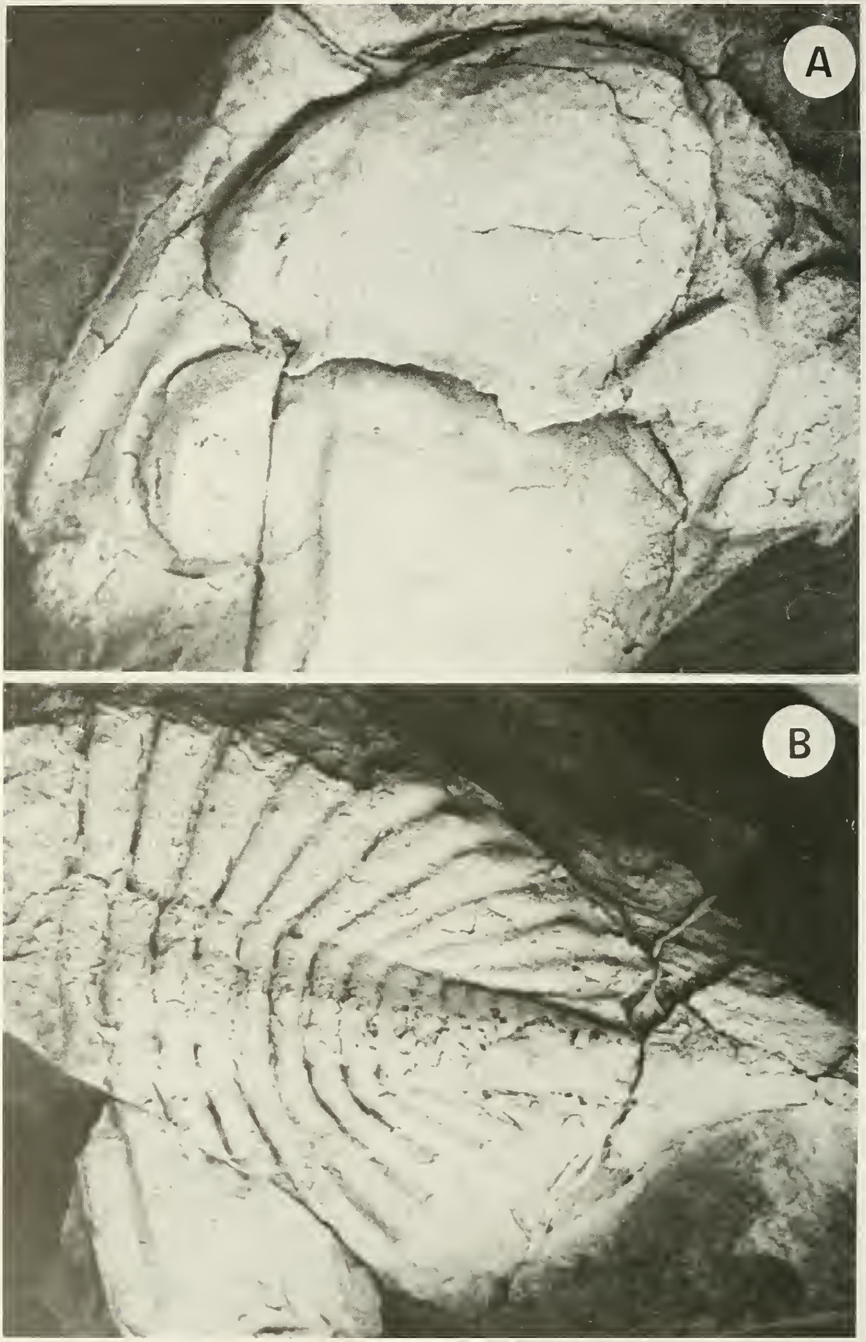

Fig. 40. *Gamonedaspis boehmi* (Knod). A. SAM–PDB4339, a fragmentary cephalon. B. SAM–PDB4332, a pygidium retaining the terminal spine. Both preserved as internal moulds and both × 2.

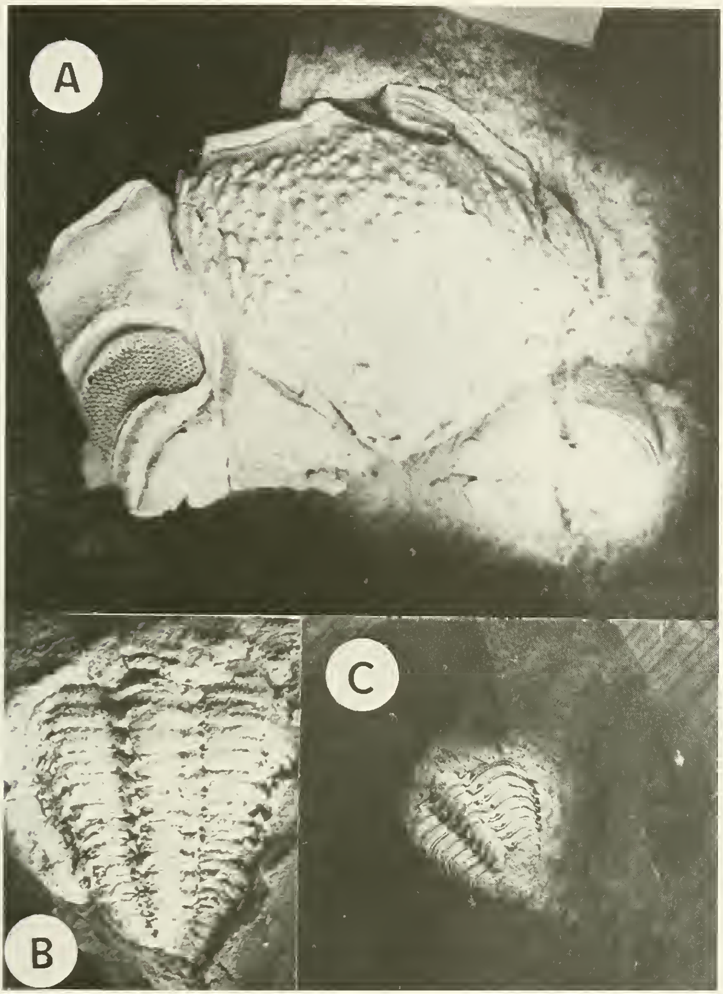

Fig. 41. A. *Gamonedaspis boehmi* (Knod). SAM–PDB4358. Note the smooth anterior border and well-developed eye socle. × 1,5. B–C. *Typhloniscus baini* (Salter). B. SAM–7799. The holotype of *Acidaspis capensis* Reed (1925*a*, pl. 11 (fig. 6)). × 1,5. C. A specimen in the South African Museum. Note the strong posterior taper of the thorax. × 1. All specimens preserved as internal moulds

Discussion

Until the full range of intraspecific variation within *G. boehmi* is documented, on the basis of a population of individuals, the largely trivial characters on which Kozlowski (1923) separated his var. *boliviensis* are meaningless and this taxon is not used here.

Gamondedaspis scutata Braniša & Vaněk differs from the present species in its uptilted post-axial spine, fewer (9–10) and narrower pleural ribs, and

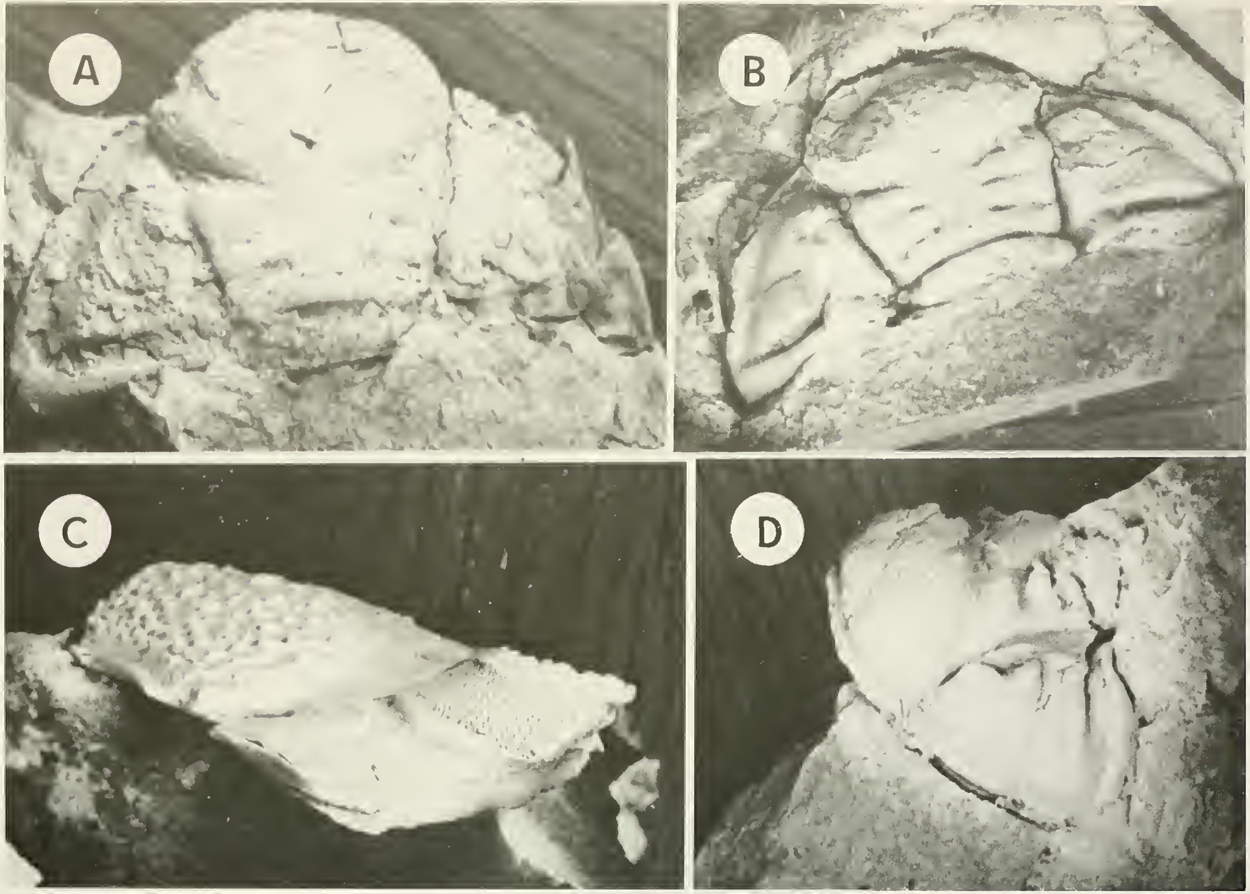

Fig. 42. A–B, D. *Metacryphaeus caffer* (Salter). A. SAM–PDB4068, an individual that approaches *M. convexus* (Ulrich) in the inflated median area of its glabella. B. A specimen in the South African Museum. D. SAM–PDB4047, showing the impression of the genal spinule. C. *Gamonedaspis boehmi* (Knod). Lateral view of the cephalon, showing the visual surface of the eye. All specimens preserved as internal moulds, and all × 2.

seemingly fewer axial rings. It is also a somewhat older species. *Gamonedaspis accola* (Clarke) (1913: 101, pl. 4 (figs 9–20)) is very close to the present species, as noted by Kozlowski (1923). So far as can be judged from Clarke's perhaps somewhat idealized drawings, it differs from *G. boehmi* only in the irregular development of the tubercles on the pygidial axis. Since this is perhaps an artefact of preservation, *G. accola* is likely to become a synonym of Knod's species.

Occurrence

Gamonedaspis boehmi (Knod) is currently known with certainty only from Bolivia and the Voorstehoek Formation of South Africa, but may also prove to be present in Brazil.

Superfamily ACASTACEA

Discussion

On the basis of Eldredge's (1979) phylogenetic analysis of this group of trilobites, the writer is inclined to recognize the following subdivisions:

- Family Acastidae
  - Subfamily Acastinae
  - Subfamily Acastavinae
- Family Asteropygidae
- Family Calmoniidae
  - Subfamily Calmoniinae
  - Subfamily Bouleiinae

These taxa are united by the form of their auxiliary impression systems which is '. . . a highly organized and distinctly triangular series of two major radiating rows of impressions (with accessory impressions in subsidiary rows), with the midline devoid of impressions, and with the widest portion of the field situated adjacent to the pre-glabellar furrow or facial suture' (Eldredge & Braniša 1980: 191).

Family **Calmoniidae** Delo, 1935

Discussion

The quite remarkable pattern of speciation among the calmoniid trilobites is undoubtedly due to adaptive radiation, causally related to marine transgression (Cooper 1977) and the niché diversity and abundance brought about by the flooding of large areas of Gondwanaland by the late Emsian–early Eifelian eustatic transgression. As such, there is likely to be a very high degree, if not complete endemicity, of the taxa involved. Hence, the writer would agree with Eldredge & Braniša (1980) in regarding the family as wholly Malvinokaffric.

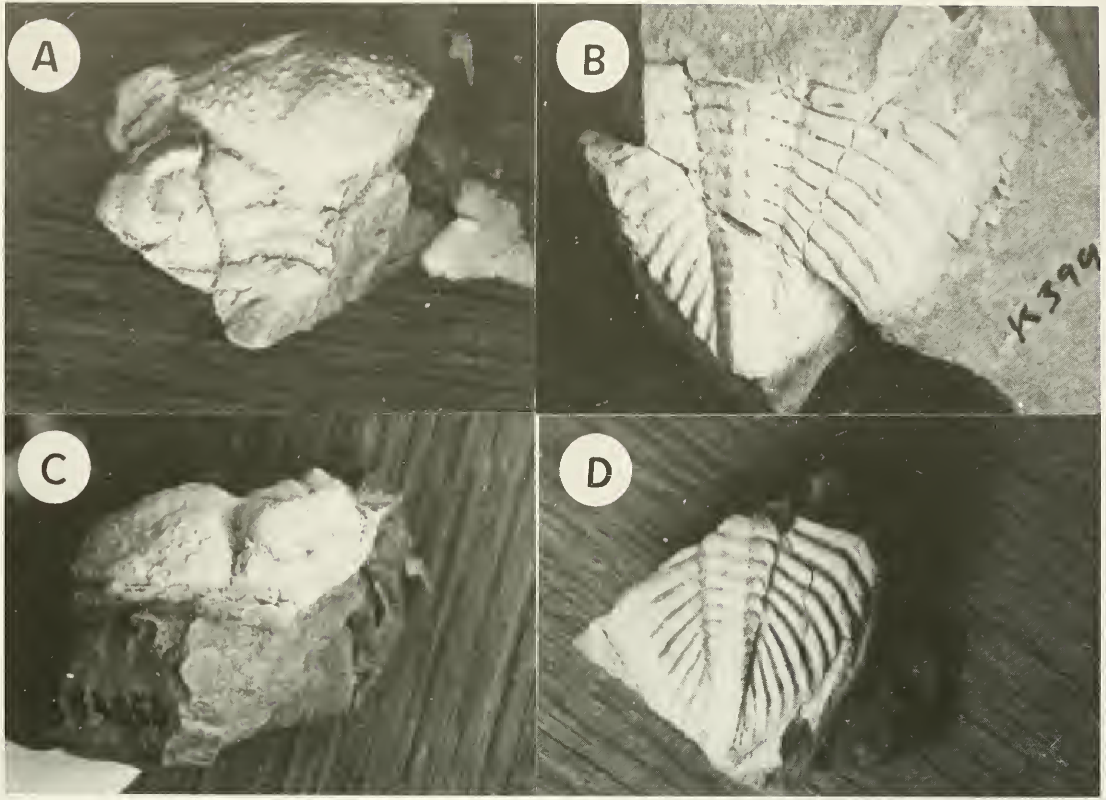

Fig. 43. *Gamonedaspis boehmi* (Knod). A, C. SAM–PDB4056. Note the transglabellar furrows and isolation of the frontal and L3 lobes. × 1,6. B. SAM–PDB 3997, showing the paired axial tubercles. × 1,5. D. SAM– PDB4336. × 1,3. All preserved as internal moulds.

Such alleged calmoniids as *Neocalmonia* (Pillet 1969) are better assigned to the family Asteropygidae, while *Dalmaniturus* is also excluded from the current concept of the family.

Hupé (1955) created the monotypic subfamily Bouleiinae, within the Phacopidae, for *Bouleia* but, as shown by Eldredge (1972), the latter genus is merely a phacopid homoeomorph whose affinities are with the Calmoniidae. As such, the Bouleiinae becomes a subfamily within the Calmoniidae. On hypostomal characters and the strong reduction of the L1 lobes, the writer is also inclined to place *Parabouleia*, *Malvinella*, and *Vogesina* in this subfamily.

Provisionally, therefore, the following taxa may be included in the subfamily Calmoniinae: the *Calmonia* plexus comprising *Calmonia*, *Paracalmonia*, *Metacryphaeus (Metacryphaeus)*, *M. (Wolfartaspis)*, *Tibagya* and *Punillaspis*, the *Phacopina* plexus of *Phacopina*, *Pennaia*, *Oosthuizenella* and *Andinacaste*, the *Probolops* group comprising *Probolops*, *Tarijactinoides*, *Renniella*, *Cryphaeoides* and perhaps *Schizostylus*, the unique *Typhloniscus*, and the group comprising *Bainella*, *Deltacephalaspis (Deltacephalaspis)*, *D. (Prestalia)*, *Kozlowskiaspis (Kozlowskiaspis)* and *K. (Romanops)*.

Genus ***Oosthuizenella*** gen. nov.

Type species *Phacops ocellus* Lake, 1904;
by original designation herein

Etymology

For Mr Roy Oosthuizen of Zwartskraal, Prince Albert, who allowed the writer to study his magnificent collection of Bokkeveld trilobites, collected and meticulously prepared over many years, and freely shared his expert knowledge of this group.

Diagnosis

Cephalon subtrigonal in outline, wider than sagittal length. Genal angles with small spiniform processes. 2p and 3p glabellar furrows subparallel and characteristically sinuous and equally impressed; 2p furrows not reaching axial furrows. 1p furrows very deep, concave anteriorly, and weakly connected to axial furrows. Frontal lobe with pronounced 'acastid' auxiliary impression system. Occipital furrow with strongly convex anterior margin and broadest sagittally. Occipital ring smooth, of constant width. Eyes small (about one-third of exsagittal length), situated between abaxial terminations of 1p and 3p furrows. Pygidium semicircular, broader than long, with 4 pairs of well-developed pleural spines and a short post-axial spine. Axis rather broad, comprising 8 rings of which the anterior 2 are most pronounced. Pleural fields with 4, perhaps 5, pleurae with deep pleural grooves.

Fig. 44. A. *Gamonedaspis boehmi* (Knod). PRV–34. ×2,8. B. *Bainella arbuteus* (Lake). SAM–7793, figured by Reed (1925*a*, pl. 9 (fig. 12)) as *Phacops (Phacopina) hiemalis* Reed. ×2,8. C. *Bainella gamkaensis* Rennie. RO–67, showing the cuticular surface of the cheek. ×3. D. *Metacryphaeus caffer* (Salter). PRV–5. ×3. Except for 44C, all preserved as internal moulds.

Discussion

Although *Phacops ocellus* Lake was originally included by Clarke (1913) in his proposal of the genus *Calmonia*, the South African material shows certain features that suggest generic separation. In all the South American species of *Calmonia* the glabella shows transverse 2p furrows that deepen adaxially and are more pronounced than the 3p furrows; there is an anterior border visible dorsally and with a short median frontal process, and there are invariably 6 pairs of pleural spines to the pygidium. In *Phacops ocellus*, however, the 3p and 2p furrows are equally developed, sinuous and parallel, without adaxial deepening of the 2p furrows, the glabellar frontal lobe overhangs the anterior border, there is no sign of a frontal process, and there are only 4 pairs of pleural spines to the pygidium.

Oosthuizenella ocellus (Lake, 1904)

Figs 45–49, 50C, 85C

Calymene blumenbachii Murchison (*non* Brongniart), 1839: 654.
Phacops (Cryphaeus) africanus Salter, 1856: 218, pl. 25 (figs 6–7, 9 only).
Phacops ocellus Lake, 1904: 207, pl. 24 (figs 9–10).
Phacops (Cryphaeus) callitris Schwarz, 1906: 393, pl. 10 (fig. 2).
Pennaia africana Shand, 1914: 24, pl. 6 (figs 1–14). Swartz 1925: 51.
Phacops (Calmonia) ocellus Lake, Reed, 1925*a*: 153.
Phacops (Pennaia) africanoides Reed, 1925*a*: 158.
Phacops (Calmonia) callitris (Schwarz) Reed, 1925*a*: 149.
Acaste (Calmonia) callitris (Schwarz) Rennie, 1930: 344, pl. 9 (fig. 19).
Acaste (Calmonia) africana (Shand) Rennie, 1930: 344.
Bainella? ocellus (Lake) Struve (*in* Harrington *et al.*), 1959: 0484, fig. 383, 2f.
Calmonia ocellus (Lake) Eldredge & Ormiston, 1979: 158.
Calmonia? callitris (Schwarz) Eldredge & Ormiston, 1979: 158.

Material

The holotype, by monotypy, of *Phacops ocellus* Lake in the British Museum, BM–In4957, together with the holotype of *Pennaia africana* Shand, SU–E417B, the holotype and paratype of *Phacops callitris* Schwarz, AM–29 and AM–34 respectively, AM–18 and RO–42, 777–778, E69, E94–95, E42–45, E61 and E66. All are preserved as internal moulds.

Description

Cephalon. The cephalon is subtrigonal in outline, convex, and about twice as wide as the sagittal length. The glabella is moderately convex, pentagonal, and with well-developed axial furrows diverging slightly to the anterior. There are weak axial furrow pits. The frontal lobe is rhomboidal, with a pronounced 'acastid' auxiliary impression system, and overhangs the anterior border slightly. The 3p and 2p furrows are equally impressed, parallel, distinctly flexuous, and directed posteromedially. The 3p furrow does not reach the axial furrow. Because the 2p furrows do not meet the axial furrows, the L3 and L2 lobes are fused distally. The 1p furrows are anteriorly concave, with deep apodemal pits, and connect weakly with the axial furrows. The occipital furrow

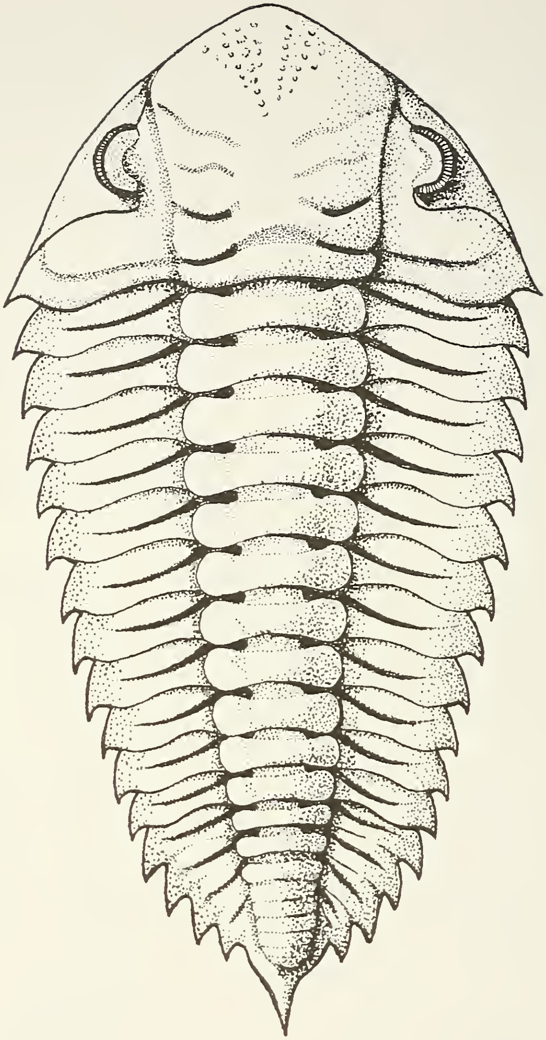

Fig. 45. *Oosthuizenella ocellus* (Lake). Reconstruction based upon the available material. × 2.

Fig. 46. *Oosthuizenella ocellus* (Lake). The holotype, BM–In4957, figured by Salter (1856, pl. 25 (fig. 6)) and Lake (1904, pl. 24 (fig. 9)). × 2.

is well developed with a strongly convex anterior border and an almost straight posterior margin, and is thus broadest sagittally. There are deep apodemal pits to the occipital furrow, immediately behind the L1 lobes. The posterior border furrows are moderately deep, shallowing abaxially, while the lateral border furrows are weakly developed and become obsolete anteriorly. The genal angles are subrounded and bear short spiniform processes. The eyes are relatively small about one-third of the exsagittal cephalic length, and situated

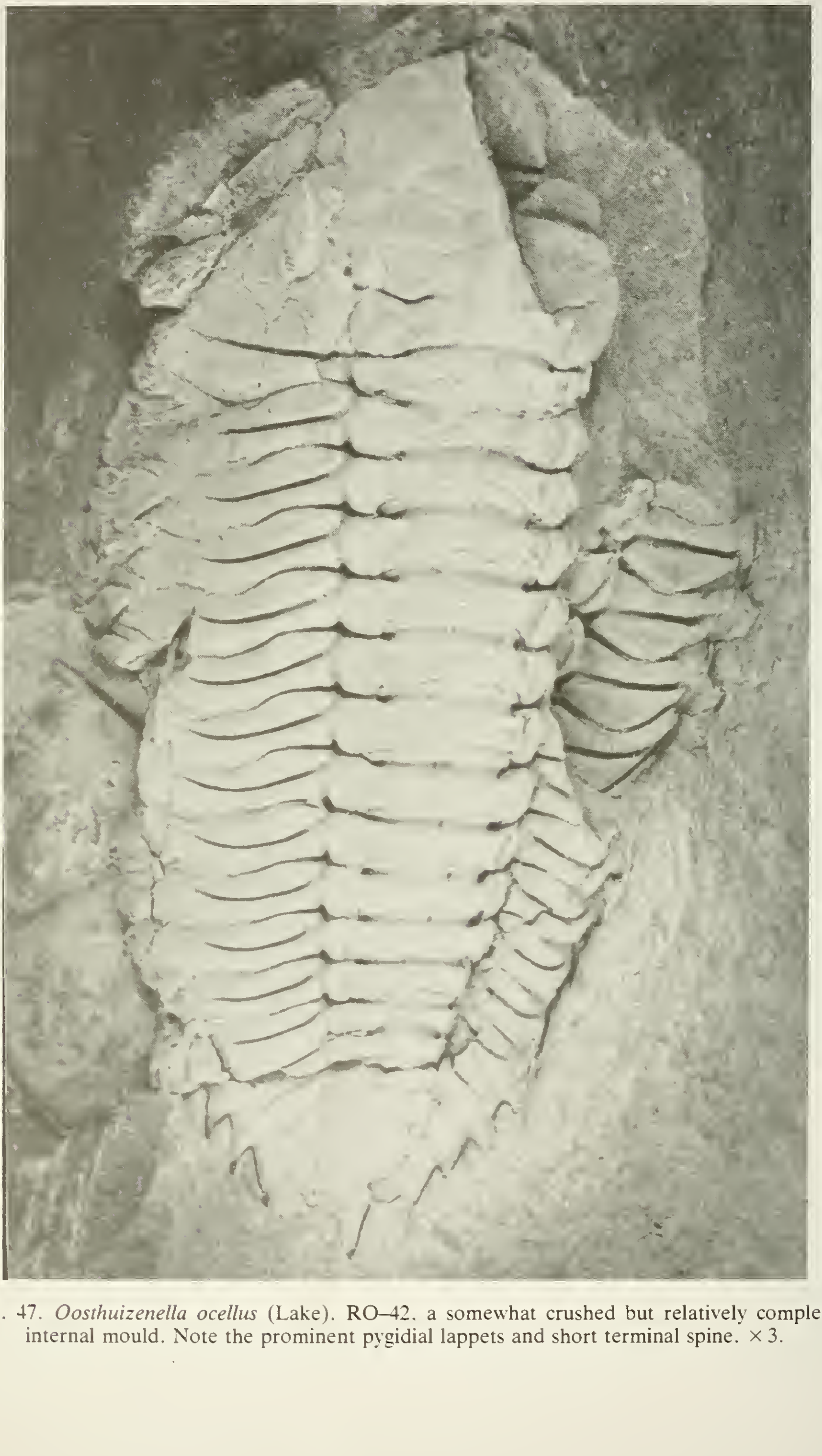

Fig. 47. *Oosthuizenella ocellus* (Lake). RO–42, a somewhat crushed but relatively complete internal mould. Note the prominent pygidial lappets and short terminal spine. × 3.

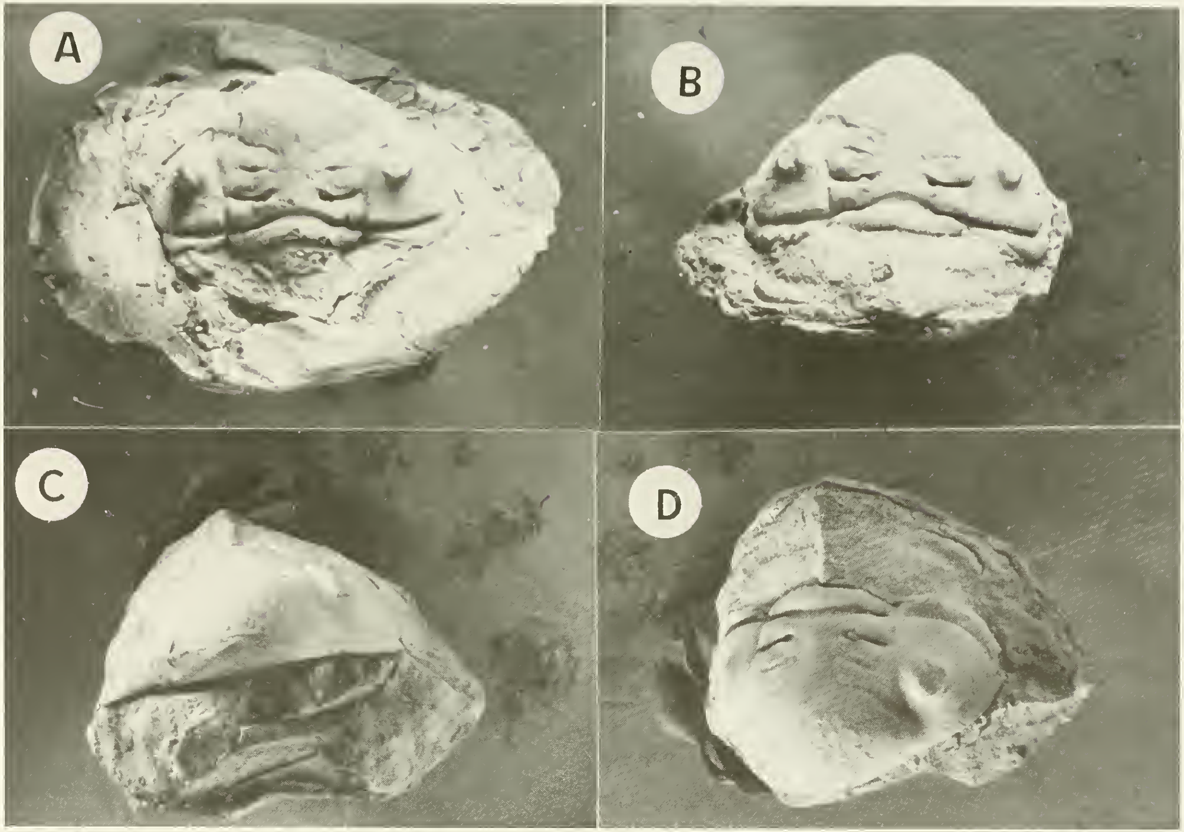

Fig. 48. *Oosthuizenella ocellus* (Lake). A. AM–34, the paratype of *Phacops callitris* Schwarz. B–D. AM–29, the holotype of *Phacops callitris* Schwarz (1906, pl. 10 (fig. 2)). Both preserved as internal moulds and both × 1,1.

Fig. 49. *Oosthuizenella ocellus* (Lake). RO–777. Posterior portion of thorax and anterior portion of pygidium, showing the distinct pleural spines. Preserved as an internal mould. ×2.8.

between the distal terminations of the 1p and 3p furrows. They comprise 23–24 vertical files, with 7–8 ocelli in the central files. The anterior branches of the facial suture just transect the lateral extremities of the frontal lobe.

Thorax. The thorax is moderately convex, with an axis about one-third the thoracic width. The axial rings are distally spatulate and separated by fairly deep ring furrows with apodemal pits developed abaxially. The axial furrows are moderately deep and distinct. The pleurae are convex, distally with short, posteriorly directed spines, and with pronounced, anteriorly concave pleural grooves that do not reach the distal extremities of the pleurae. The interpleural furrows are moderately developed.

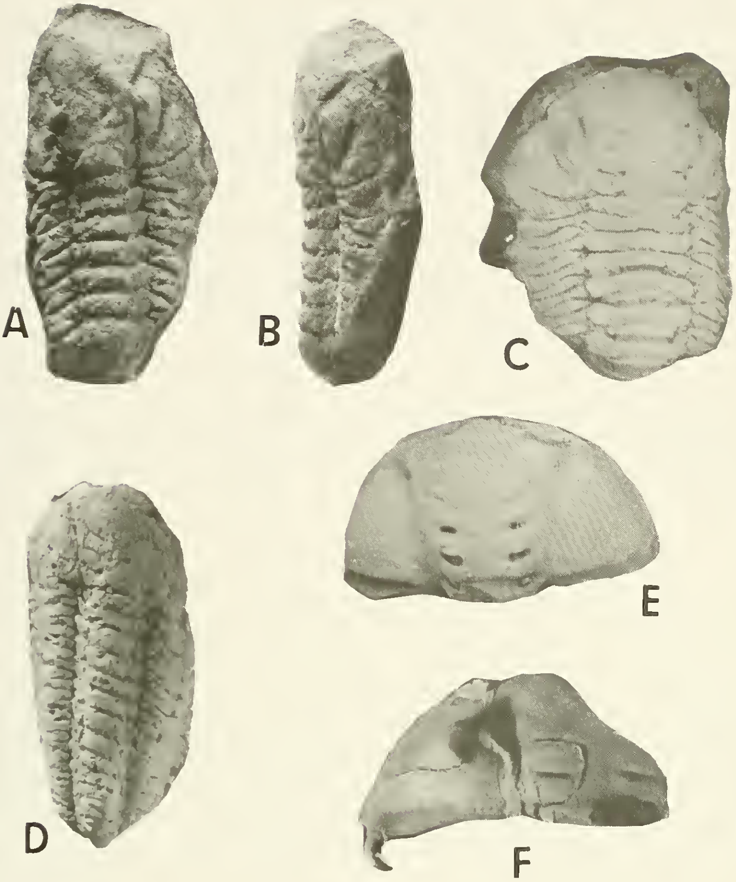

Fig. 50. A–B. aff. *Pennaia* sp. AM–25, one of Schwarz's (1906) syntypes of *Phacops gydowi*. C. *Oosthuizenella ocellus* (Lake). SU–E417B, the holotype of *Pennaia africana* Shand (1914. pl. 6 (figs 1–4)), renamed *Phacops (Pennaia) africanoides* Reed (1925*a*). D. *Pennaia?* sp. AM–26, selected by Schwarz (1906) as the type for the body of *Phacops gydowi* Schwarz. E. *Typhloniscus baini* Salter. SU–K463. F. *Bainella africana* (Salter). RO–784. All preserved as internal moulds and all × 1.

Pygidium. The pygidium is subtrigonal in outline, almost semicircular, convex, and with a pronounced axis. The latter comprises 8 rings, of which only the anterior 2 are separated by well-developed ring furrows. The axis tapers posteriorly for the first 3 rings, after which the axial furrows become subparallel, and is bluntly rounded posteriorly. The pleural fields are gently convex and comprise 4, perhaps 5, pleurae, each with deep pleural grooves and faint interpleural furrows. The pleurae terminate in well-developed, short, posteriorly directed spines of which there are 4 on either margin. There is a short, pointed post-axial spine.

Discussion

This species differs from all described species of *Calmonia* in features of the glabellar segmentation and in possessing only 4 pairs of pleural spines to the pygidium. It is also close to *Pennaia pupillus* (Lake) but the latter species lacks spiniform processes to the genal angles, has transverse 2p glabellar furrows which deepen adaxially, possesses fewer axial rings and pleurae to the pygidium, with only 3 pairs of minute pleural spines, and lacks a terminal spine.

The material assigned by Clarke (1913, pl. 5 (figs 10–15)) to this species differs in possessing deep, transverse 2p furrows and at least 5 pairs of pleural spines to the pygidium. According to N. Eldredge (*in litt.* 1980), this material *is* assignable to *Oosthuizenella.*

Occurrence

Oosthuizenella ocellus (Lake) is currently known with certainty only from the Gydo Formation, but may be present in the Falkland Islands.

Genus *Pennaia* Clarke, 1913

Type species *Pennaia pauliana* Clarke, 1913;
by original designation

Discussion

Eldredge & Braniša (1980) have recently discussed the Malvinokaffric species of *Acastoides*, noting that they differ from the Boreal species (which include the type of the genus) in having (i) shorter and narrower pygidia, (ii) a prominent axis, bluntly rounded posteriorly and with a distinct post-axial field, (iii) a less well-differentiated palpebral complex, and (iv) the posterior borders of the cephalon strongly convex so that the genal angles are situated opposite the posterior margins of the eyes. Moreover, they noted, as had Kozlowski (1923), that in well-preserved material there were small lappets to the anterior three pleurae of the pygidium. In the latter character, '*Acastoides*' *verneuili* (d'Orbigny) is obviously allied to *Pennaia* and was, in fact, assigned to this genus by Reed (1927). It is highly significant, therefore, that the Bolivian '*Acastoides*' species differ from the type species of *Acastoides* in having well-developed L1 lobes to the glabella and a hypostoma with the maculae situated on the anterior margin of the middle body, not laterally as in *A. henni* (Richter). In consequence, the Bolivian '*Acastoides*' species are here transferred to *Pennaia* although the strongly convex posterior border of *P. verneuili* (d'Orbigny), with the concomitant shift in position of the genal angles, the pronounced auxiliary impression system and the anteriorly convex form of the 2p glabellar furrows, may prove to warrant subgeneric separation. As such, *Pennaia* should be regarded as a synchronic Malvinokaffric homoeomorph of the Boreal *Acastoides*.

Pennaia pupillus (Lake, 1904)

Figs 6C, 51–55, 56C–G, 58E–F, 59C–D, 99D

Phacops pupillus Lake, 1904: 203, pl. 24 (fig. 1).
Phacops impressus Lake, 1904: 209, pl. 25 (fig. 1).
Phacops (Cryphaeus) gydowi Schwarz, 1906: 396, pl. 10 (fig. 3).
Phacops (Calmonia) impressus Lake, Reed, 1925*a*: 150.
Phacops (Calmonia) impressus var. *vicina* Reed, 1925*a*: 151, pl. 11 (fig. 8).
Phacops (Calmonia?) pupillus Lake, Reed, 1925*a*: 156.
Phacops (Pennaia) gydowi Schwarz, Reed, 1925*a*: 157, pl. 9 (fig. 7), pl. 11 (fig. 2).
Acaste (Pennaia) impressus (Lake) Rennie, 1930: 338, pl. 9 (figs 5–13).
Metacryphaeus? pupillus (Lake) Eldredge & Ormiston, 1979: 160.
?Phacops (Cryphaeus) africanus Salter, 1856: 218, pl.25 (figs 2, 9c, 10, 13 only).

Material

The holotype, by monotypy, SAM–K60, together with SAM–1167, 2463, 7187, 8959, 8961, 8963, 8966–8967, 8969, 9605, PDB3078, PRV–37, 3200, AM–26, 28, 69, KM–418, BM–52061, In28613–28614, 28616, 28618–28619, IM29236, and RO–4, 213, 273, 704, 758, 762, 774, 781, 791, 797, 831, C70, E26, 28, 78–79, L76, and P2.

Description

Cephalon. The cephalon is rather convex, subtrigonal in outline and about twice as wide (trans.) as the sagittal length. The glabella is moderately convex, subpentagonal, widening slightly to the anterior and typically with a rhomboidal frontal lobe. The auxiliary impression system is poorly developed and only occasionally visible, e.g. PRV–3200. The axial furrows are well defined, subparallel, and with prominent axial furrow pits opposite the distal terminations of the 3p furrows. The latter are moderately impressed, straight to very slightly sinuous, and distinctly connected to the axial furrows. The 2p furrows are deep, transverse, and distally obsolete, so that L2 and L3 coalesce distally. The 1p furrows are very deep, directed slightly posteromedially, and distinctly connected to the axial furrows. There is a slight forward curvature of the adaxial ends of the 1p furrows as well as a weak, but distinct adaxial bifurcation well seen in the lectotype. The L1 lobes broaden abaxially. The cheeks are subtrigonal, moderately convex and down-turned and apparently lacking spiniform processes. The posterior border furrows are deep, transverse, becoming shallower distally, whereas the lateral border furrows are shallow and poorly defined. The anterior border is very narrow, and generally obscured dorsally by the frontal lobe. The occipital furrow is rather deep, anteriorly convex, widest sagittally, and with deep apodemal pits distally. The smooth occipital ring is of more or less constant width, and the posterior borders broaden (exsag.) slightly towards the genal angles which are subrounded. The eyes are rather large, somewhat more tha one-third of the exsagittal cephalic length. The visual surface comprises 28–29 vertical rows of ocelli, with 7–8 lenses in the middle row. The anterior branch of the facial suture only just transects the lateral extremities of the frontal lobe (fig. 54),

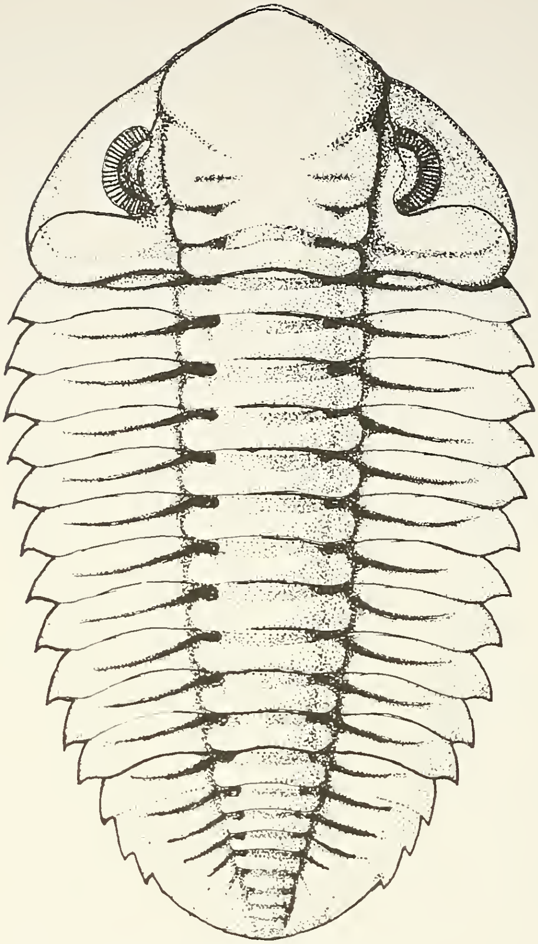

Fig. 51. *Pennaia pupillus* (Lake).
A reconstruction based upon
the available material. × 2.

while the posterior branches meet the lateral margins more or less in line with posterior ends of the eyes.

Thorax. The thorax is strongly convex, with an axis about one-third of the thoracic width. The axial rings are distally spatulate and separated by rather deep intersegmental grooves that bear apodemal pits distally. The pleurae are convex, with deep, anteriorly concave pleural grooves that taper distally and become obsolete before reaching the distal extremities of the pleurae. The latter are ornamented with minute, posteriorly directed spines.

Pygidium. The pygidium is semicircular to subtrigonal in outline, moderately convex, and with an axis composed of 8–10 rings. The axis tapers uniformly to the posterior and there is no post-axial field. The pleural fields are gently convex and comprise 5, possibly 6, pairs of pleurae, each with deep, well-defined pleural grooves that become obsolete before reaching the pygidial border. Distinct interpleural furrows are developed only between the anterior pleurae; posteriorly they are only faintly visible mesially. Like the pleural grooves, the interpleural furrows are distally obsolete, so the pygidium is left with a smooth border. The pygidial margin is ornamented with 3 (? occasionally 4, *fide* Rennie 1930) pairs of very short, broad, triangular spines that are directed posteriorly and correspond with the anterior 3 pleurae. Behind these spines the pygidial margin is entire.

Discussion

Lake (1904) considered the holotype of *Phacops pupillus* to have spiniform processes to the genal angles but, as can clearly be seen from Figure 52, this is an artefact of preservation. The posterior border of the left cheek of the holotype has been broken off for almost its entire length, save for a small, narrow remnant at the genal angle; this gives the erroneous impression of a spiniform process to the genal angle.

In creating *Phacops impressus*, Lake (1904: 209) noted that ' . . . this form is represented by several nearly complete specimens, but they are so much crushed and distorted that it is impossible to determine accurately the characters of the head'. Since then, however, Rennie (1930) has provided an excellent description of this species, based upon well-preserved topotype material, and it is now clear that *P. pupillus* and *P. impressus* were originally based upon different parts of the same animal. Unfortunately, because of page priority, the better known *Pennaia impressus* (Lake) must become a junior subjective synonym of *P. pupillus*.

A perturbing feature of the *Pennaia* material from the Bokkeveld succession is that few examples have identical cephala (Fig. 59), but seemingly all have identical thoraxes and pygidia. On the basis of current taxonomic practice within the group, a number of these could perhaps be given new specific names. However, the writer is not yet certain that more than a single, highly variable, polytypic species is present. Thus, PRV–3100 (Fig. 58E–F) differs from typical *P. pupillus* in having the posterior borders arched strongly forward so that the genal angles, which are acuminate, are situated opposite the posterior portions of the eyes. This specimen also has relatively somewhat smaller eyes than typical *P. pupillus*, and with a broader frontal lobe. The glabellar segmentation is also somewhat more deeply impressed and the 2p furrows are not quite transverse. It thus approaches an unnumbered specimen in the South African Museum (Fig. 99D) that differs in having transverse 2p furrows and a relatively broader (trans.), almost elliptical frontal lobe. The latter example approaches a specimen in the British Museum (Fig. 62B) that shows a similar frontal lobe, but now with a distinct auxiliary impression system and similar 2p furrows, but this specimen now has a transverse posterior border, thus resembling typical *P. pupillus*. From the latter it differs, however, in having a relatively broader,

Fig. 52. *Pennaia pupillus* (Lake). The holotype, by monotypy, SAM–PDB60, which retains cuticle. Note the pseudo-spiniform process formed by the destruction of the posterior border, the distinct posterior branch to the 1p furrow, and the strong homoeomorphic resemblance to *Phacopidina* in lateral view. × 4.

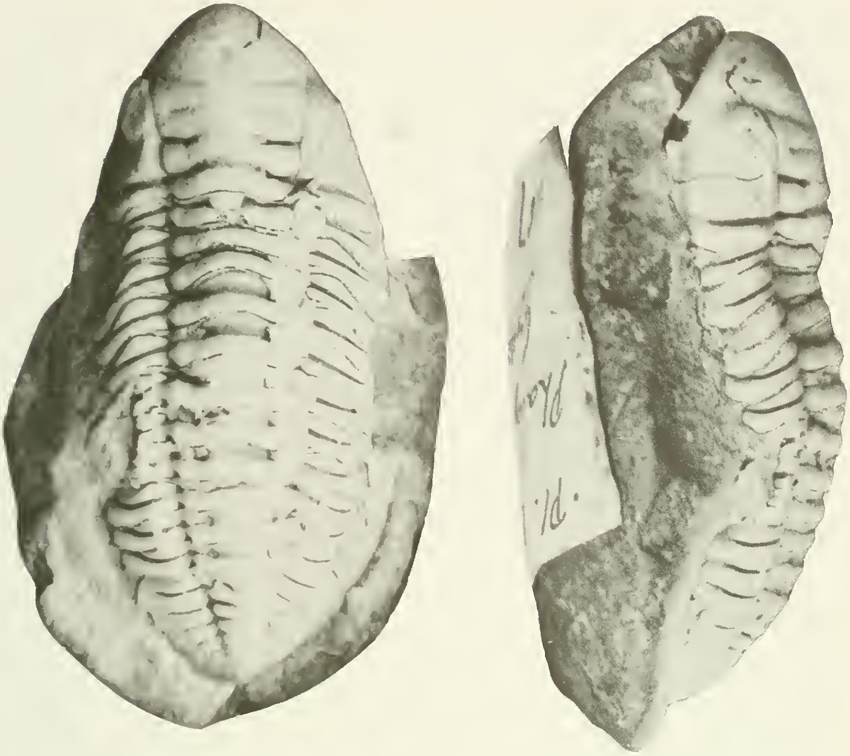

Fig. 53. *Pennaia pupillus* (Lake). SAM–1167, figured by Reed (1925*a*, pl. 9 (fig 7)), and preserved as an internal mould. × 2.

ellipsoidal frontal lobe with a distinct auxiliary impression system and 1p furrows that do not show adaxial bifurcation. *Phacopina lakei* (Reed) differs from *Pennaia pupillus* in its very much broader (trans.), elliptical frontal lobe, with the anterior border distinctly visible in dorsal view. It also has less deeply impressed 2p and 3p furrows, 2p furrows that are anteriorly convex, narrower L1 lobes, and posterior borders that curve weakly forward (Fig. 59A). Until very much bigger collections are available for study, the writer prefers to subscribe most of the above differences to intraspecific and ontogenetic variation. This tends to be supported by their sympatric association and the fact that only one type of thorax and pygidium can, at present, be identified.

Pennaia pauliana Clarke (1913: 133, pl. 5 (figs 18–25)) is very similar to the present species but was said to have only 3–4 well-defined axial rings to the pygidium, whereas in *P. pupillus* there are 8–10. Furthermore, the pleural grooves of the thorax of *P. pauliana* are not anteriorly concave as in the South African species. Although the differences are slight, the author prefers to maintain *P. pauliana* as distinct until it is revised on the basis of type and topotype material.

Fig. 54. *Pennaia pupillus* (Lake). SAM–8969a. preserved as an internal mould. Note how the anterior ramus of the facial suture transects the extreme lateral margin of the frontal lobe. × 4.1.

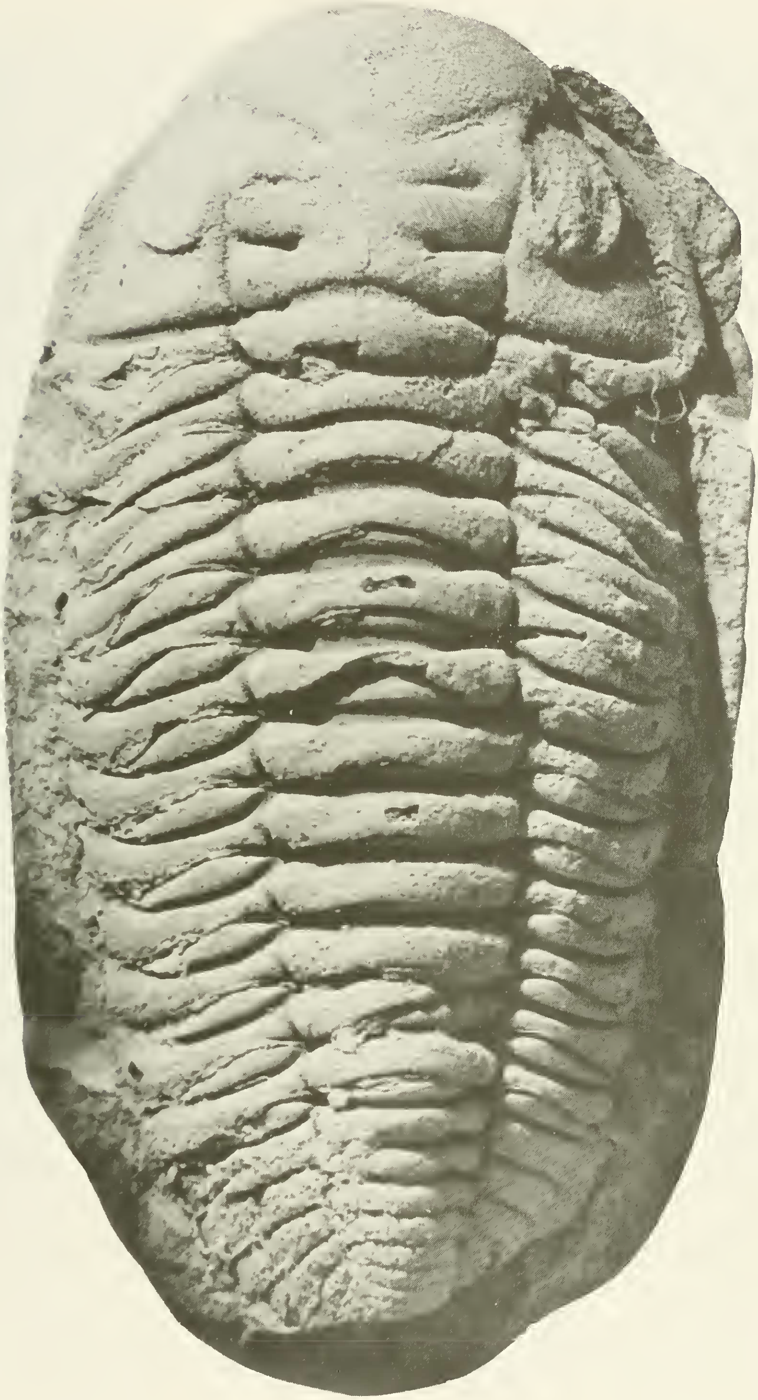

Fig. 55. *Pennaia* cf. *pupillus* (Lake). SAM-8961, preserved as an internal mould. Note the oval shape to the frontal lobe. × 4.

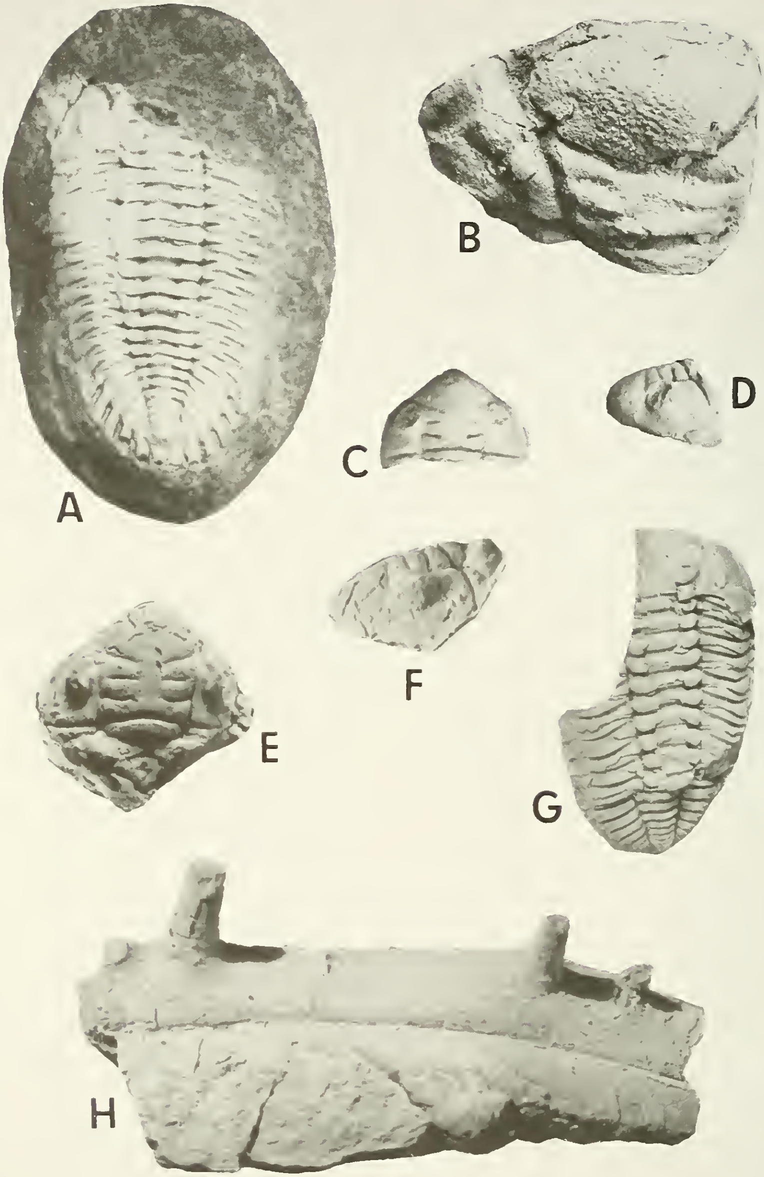

Fig. 56. A–B. *Metacryphaeus caffer* (Salter). A. SAM–PDB4345. × 1.5. Note the length and shape of the pleural lappets to the pygidium. B. SAM–PDB7787. × 1. C–G. *Pennaia pupillus* (Lake). C–D. SAM–PDB3078. × 1. E–F. AM–28, the holotype of *Phacops gydowi* Schwarz (1906, pl. 10 (fig. 3)). × 1. G. KM–418, the original of Reed (1925*a*, pl. 11 (fig. 8)). × 1. H. *Burmeisteria herscheli* (Murchison). A specimen in the South African Museum retaining spines to the thoracic axial ring. × 2. All specimens preserved as internal moulds.

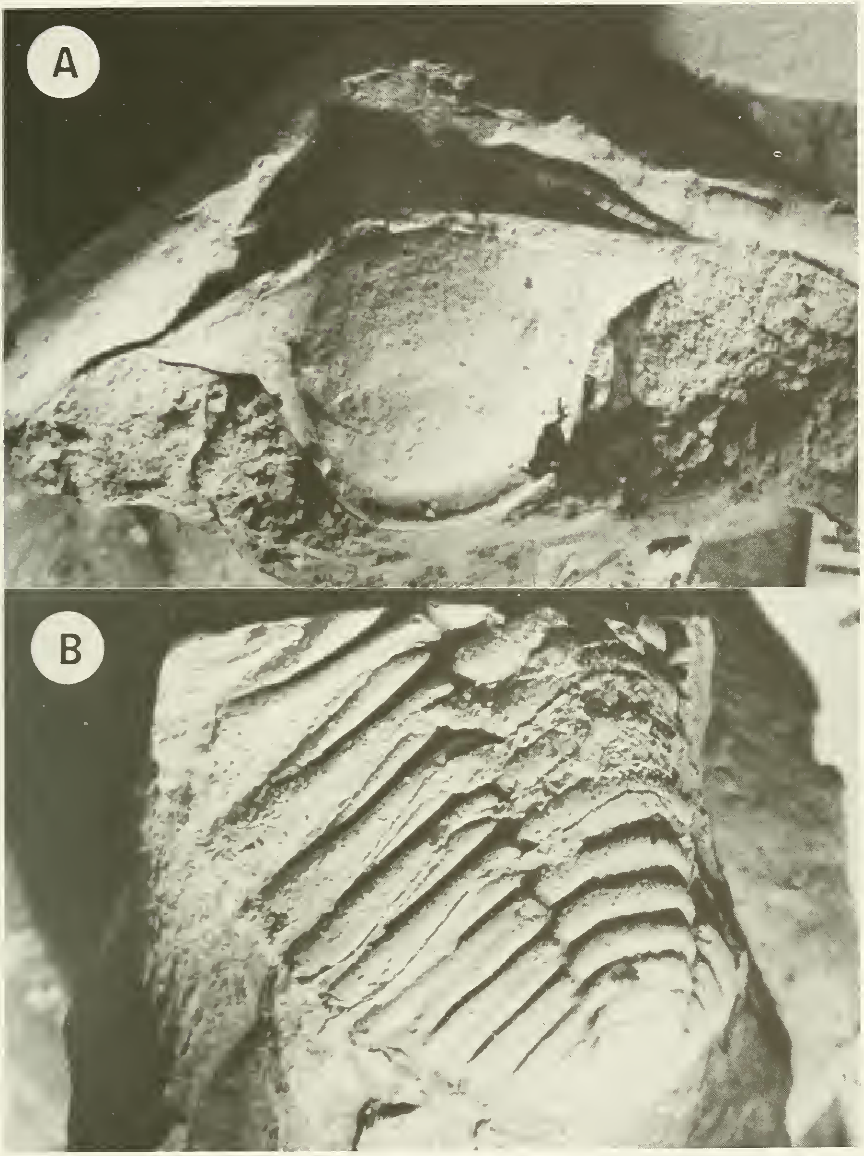

Fig. 57. A. *Bainella africana* (Salter). SAM–PDB3080, the internal mould of an hypostoma. × 4. B. *Pennaia* sp. SAM–11915, the posterior portion of the thorax and terminally eroded pygidium, preserved as an internal mould. × 4.

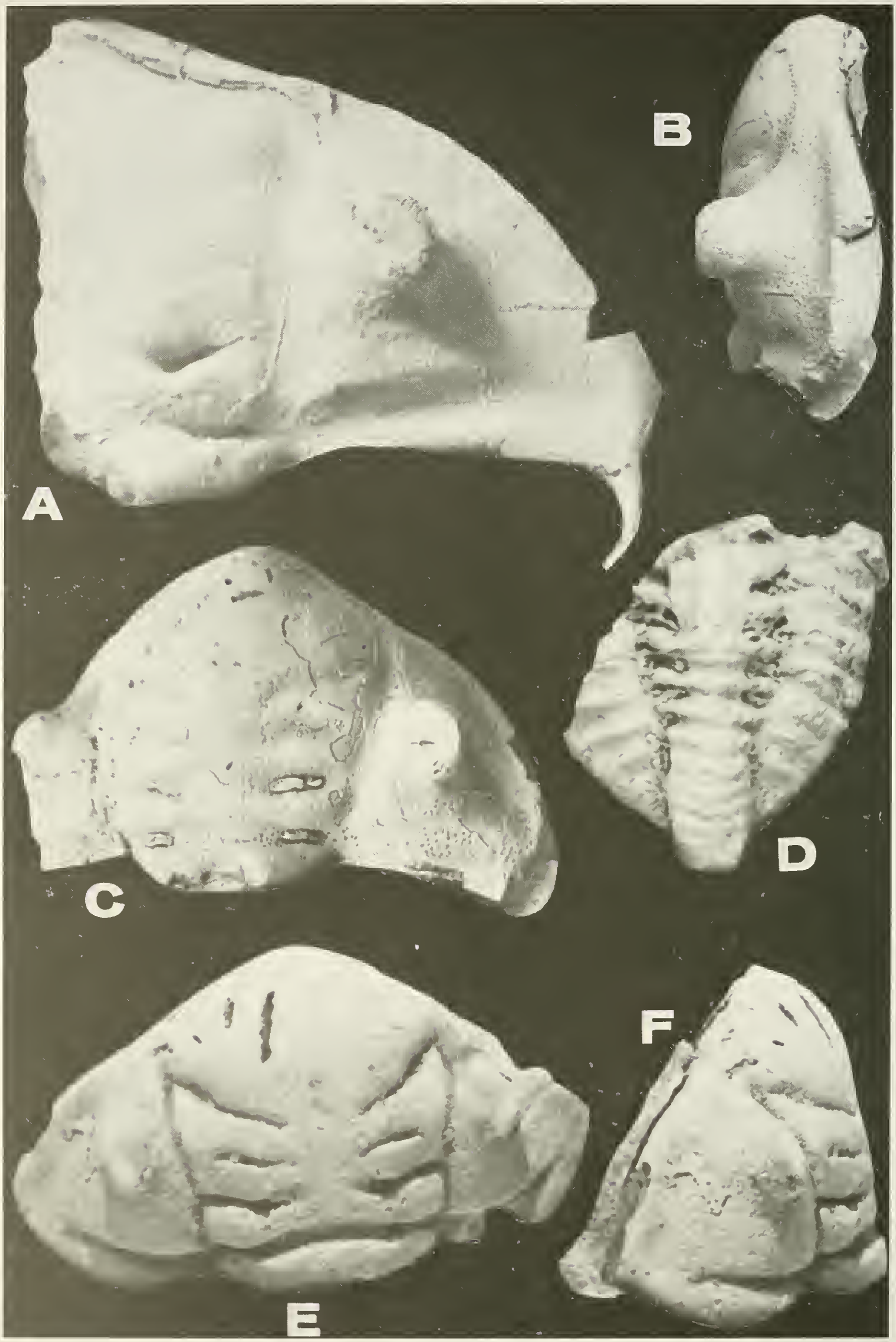

Fig. 58. A–D. *Bainella africana* (Salter). A. RO–30. × 2. B–C. SAM–782, the original of Lake (1904, pl. 24 (fig. 6)). × 2. D. SAM–PDB3945. × 2. E–F. *Pennaia* aff. *pupillus* (Lake). PRV–3100. Note the strongly curved posterior border and acuminate genal angles. × 2,7.

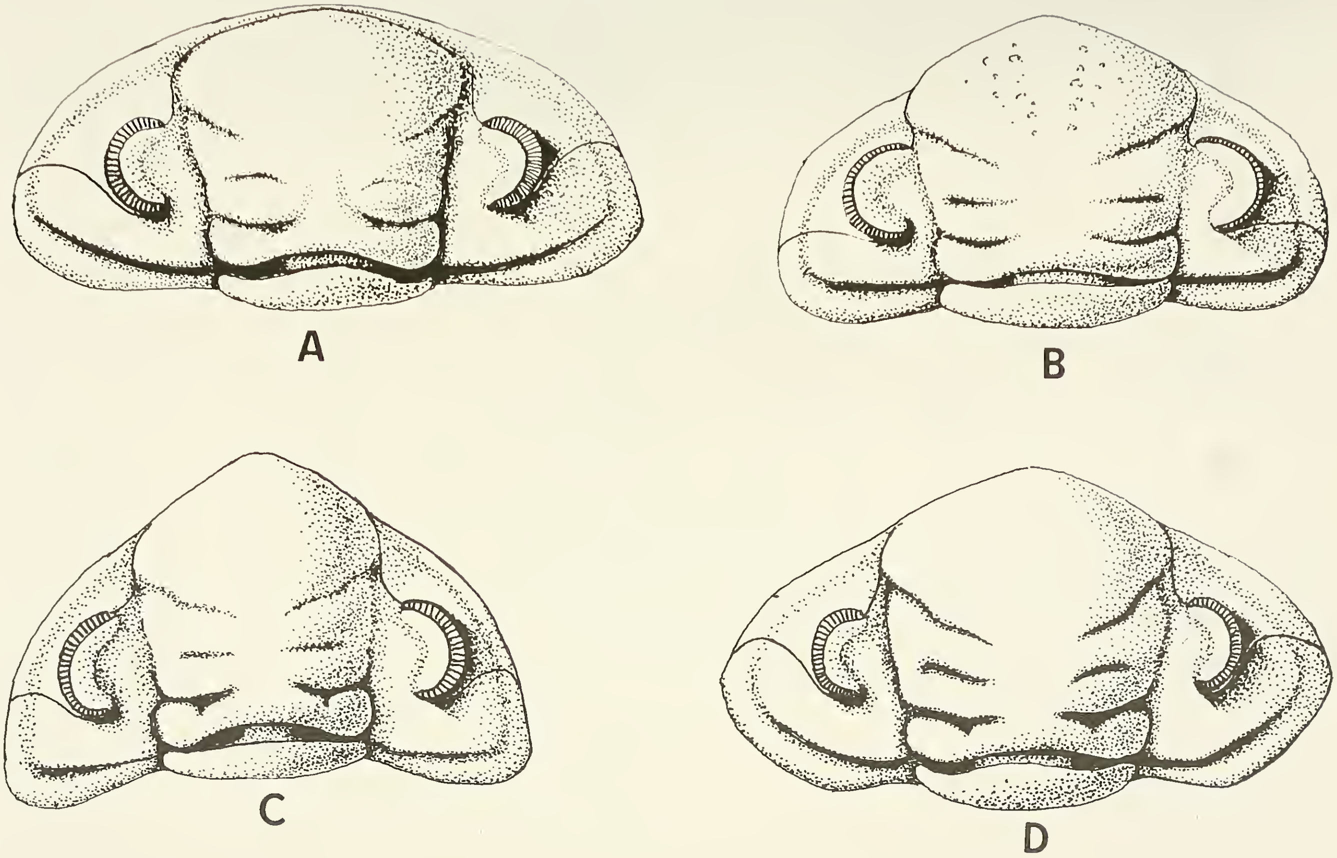

Fig. 59. Comparison of some reconstructed *Pennaia* and *Phacopina* cephala. A. *Phacopina lakei* (Reed). B. *Phacopina?* sp., the original of Salter (1856, pl. 25 (fig. 10)). C. *Pennaia pupillus* (Lake). D. *Pennaia* aff. *pupillus* (Lake), based upon PRV–3100. All reconstructed from internal moulds and all approx. × 3.

'*Acastoides*' *koukharskii* Baldis & Longobucco (1977*b*: 171, figs 1–3) is neither an *Acastoides* nor a *Pennaia*. It differs from both these genera in having 2p furrows that connect with the axial furrows and L2 lobes that narrow (exsag.) abaxially.

Pennaia gamonedensis (Eldredge & Braniša) (1980: 237, fig. 19) differs from *P. pupillus* in having smaller eyes, lightly impressed 2p and 3p furrows, the latter almost transverse, and with a pygidium with only 2 distinct axial rings and 4 pleural grooves.

Occurrence

Pennaia pupillus (Lake) is known with certainty only from the Gydo Formation, although there is a single pygidium, PRV–39, in green shale preservation that may be from the Voorstehoek Formation.

Genus *Metacryphaeus* Reed, 1907

Subgenus *Metacryphaeus* Reed, 1907

Type species *Phacops caffer* Salter, 1856;
by the subsequent designation of Rennie, 1930

Discussion

Wolfart (1968) recognized two species groups within *Metacryphaeus*; the group of *M. caffer* was said to comprise *M. caffer* (Salter), *M. australis* (Clarke), *M. praecursor* Wolfart, and *M. venustus* Wolfart, and characterized by a comparatively small exoskeleton, relatively large eyes and a limited capacity for spine formation. The group of *M. giganteus* was said to comprise *M. giganteus* (Ulrich), *M. convexus* (Ulrich), *M. dereimsi* (Groth), *M. boulei* (Kozlowski), *M. cornutus* Wolfart, and *M. tuberculatus* Kozlowski, and typified by the relatively larger size of the exoskeleton, relatively smaller eyes, and a marked capacity for spine formation.

The writer finds this division of little practical use since *M. tuberculatus* is a probable synonym of *M. caffer*, while *M. caffer* is very closely related to, and probably descended from *M. giganteus*, as well as being of a comparable size. It is pertinent to note, however, that Eldredge & Braniša (1980) report the presence of two distinct types of hypostomata among *Metacryphaeus* species.

Among the large number of *Metacryphaeus* species now known, one species stands alone. This is *M. cornutus* Wolfart (1968: 95, pl. 12 (figs 2–5), pl. 13 (figs 1–4), pl. 14 (figs 1–2) (Fig. 60 herein), which can be distinguished from all other described species of *Metacryphaeus* in the possession of a cylindrical terminal spine to the pygidium and a thick, cylindrical median spine to the occipital ring. It is accordingly made the type species of the new subgenus *M. (Wolfartaspis)*.

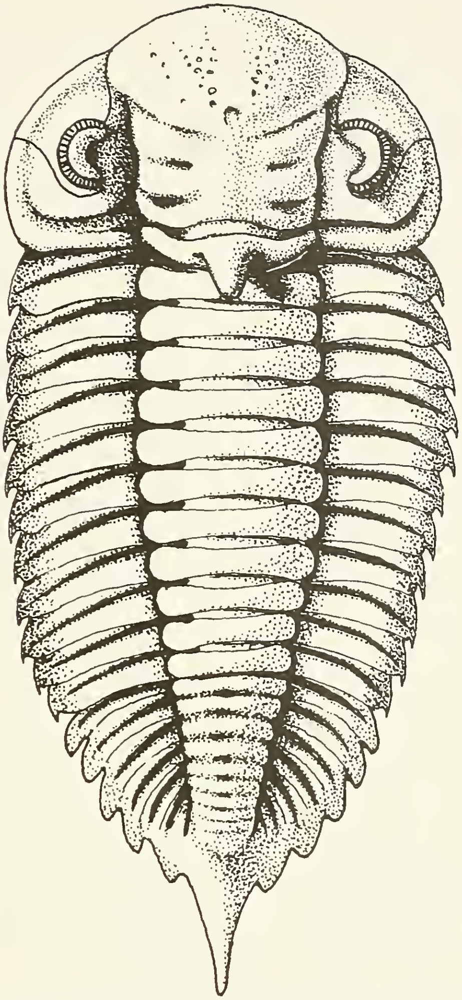

Fig. 60. *Metacryphaeus (Wolfartaspis) cornutus* Wolfart.
A reconstruction based upon the figured material. Approx. × 1,5.

Metacryphaeus (Metacryphaeus) caffer (Salter, 1856)

Figs 6D, 33A, C, 34B, 39F, 42A–B, D, 44D,
56A–B, 61, 62A, 63–64, 65C–D, 66A, 67A,
68B, 69–70, 78D, 98A, C, 99C

Phacops caffer Salter, 1856: 219, pl. 25 (figs 11–12 only).
Phacops (Cryphaeus) africanus Salter, 1856: 218, pl. 25 (fig. 4 only).
Phacops (Cryphaeus) caffer Salter, Lake, 1904: 210, pl. 25 (figs 3–4). Schwarz, 1906: 395. Clarke, 1913: 72.
Dalmanites (Cryphaeus) caffer (Salter) Reed, 1925*a*: 139, pl. 9 (figs 10–11), pl. 11 (fig. 4).
Dalmanites (Cryphaeus) caffer var. *albana* Reed, 1925*a*: 144, pl. 11 (fig. 1).
Dalmanites (Cryphaeus) cf. *australis* (Clarke) Reed, 1925*a*: 146, pl. 11 (fig. 9).

Dalmanites (Cryphaeus) cf. *pentlandi* (Salter) Reed, 1925*a*: 146, pl. 11 (fig. 10).
Dalmanites (Cryphaeus) caffer (Salter) var., Reed, 1925*a*: 145.
Dalmanites (Corycephalus?) capensis Reed, 1925*a*: 131, pl. 8 (figs 5–6).
Dalmanites (Eocorycephalus) capensis Reed, 1925*b*: 133.
Asteropyge caffer (Salter) Reed, 1927: 310.
Dalmanites (Metacryphaeus) caffer (Salter) Rennie, 1930: 336, pl. 9 (figs 3–4).
Metacryphaeus caffer (Salter) Reed, 1907: 168. Struve (*in* Harrington *et al.*), 1959: 0484, fig. 383, 3c. Wolfart, 1968: 81. Eldredge & Ormiston, 1979: 159.
? Dalmanites (Cryphaeus?) cf. *rostratus* Kozlowski, Reed, 1925*a*: 147, pl. 8 (fig. 2).
? Dalmanites (Proboloides) ensifer Reed, 1925*a*: 136, pl. 8 (fig. 4).
? Schizostylus ensifer (Reed) Wolfart, 1968: 113.
? Schizostylus (Curuyella) ensifer (Reed) Eldredge & Ormiston, 1979: 159. Eldredge & Braniša, 1980: 228.

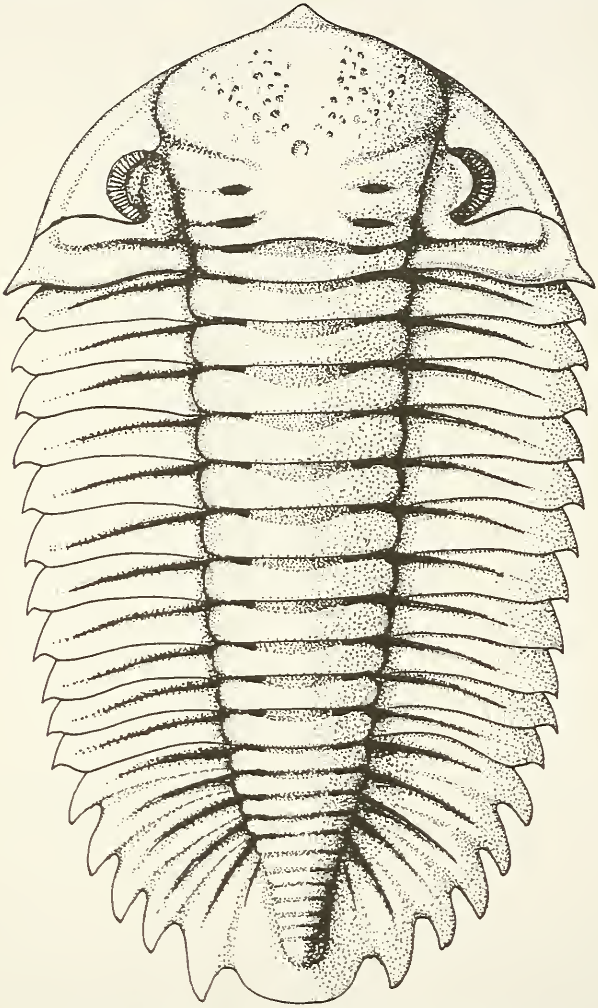

Fig. 61. *Metacryphaeus (Metacyphaeus) caffer* (Salter).
A reconstruction based upon the available material.
Approx. × 1,5.

Material

Numerous specimens including the lectotype, BM–In28620 (Fig. 62A), and BM–28783, BM–It1619, ?SMC–A3063, SAM–PDB2463, 3088, 3850, 3943, 4000, 4041, 4047, 4068, 4075, 4078, 4329, 4335, 4340–4341, 4346–4347, 4350–4352, 4354, 4363, 7184–7185, 7788–7790, 7792, 7799, 11900, PRV–5, 922, 1028, 1070, AM–74, SU–C2, 13, SU–H73, 76, 172–3, SU–E414, 483, together with RO–68, 207, 241, 285, 703, 820–828, 833, E60, 77, 93, and 96.

Description

Cephalon. The cephalon is moderately convex, semicircular to semi-elliptical in outline, and more than twice as wide as the sagittal length. The glabella expands evenly towards the anterior with deep, straight axial furrows. The inflated frontal lobe is coarsely pitted by internal muscle scars, and there is a well-developed posterior median impression. The 3p furrows are strongly developed, directed posteromedially at about 60° to the axial furrows and distinctly connected to the latter. The 2p furrows are transverse, deepest adaxially, and only very weakly connected to the axial furrows. The 1p furrows are normal to the axial furrows and thus directed slightly anteromedially, with the result that the L1 lobes tend to have a uniform width (exsag.). They have deep apodemal pits adaxially and are slightly more strongly connected to the axial furrows than the 2p furrows. The occipital furrow is rather deep, with abaxial apodemal pits, and a moderately convex anterior margin but an almost transverse posterior border, with the result that it is broadest sagittally. The occipital ring is of uniform width, straight, transverse, and wider (sag.) than the occipital furrow. The posterior border furrows are rather broad (exsag.) and deep, and meet the moderately developed lateral border furrows in acute angles at the genal angles which bear short spiniform processes. The anterior border furrow is very shallow and weakly developed but there is a short but distinct uptilted median frontal process. The cheeks are subtrigonal in outline and moderately convex. The eyes are moderately large, about one-third of the exsagittal length, and comprise 23–27 vertical files of lenses, with 8–9 lenses in the central file. The eyes are strongly arcuate, with distinct palpebral furrows, and touch the axial furrows anteriorly immediately behind the abaxial terminations of the 3p furrows. The posterior borders of the eyes lie in a plane slightly anterior to the distal terminations of the 1p furrows.

Thorax. The thorax is moderately convex, with an axis about one-third the thoracic width. The axial rings are distally spatulate and separated by moderately wide, deep, ring furrows with abaxial apodemal pits. The axial furrows are deep and well defined. The pleural fields are moderately convex, with pronounced fulcra at about the middle of their transverse widths. The prominent deep pleural grooves are almost straight, tapering distally and becoming obsolete before the abaxial terminations of the pleurae are reached. The latter bear small, posteriorly directed spines. The interpleural furrows are well developed, narrower than the pleural grooves, deepest adaxially, and show distinct geniculations at the fulcra.

Pygidium. The pygidium is almost semicircular in outline, distinctly wider than the sagittal length, and moderately convex. The axis is broad anteriorly and tapers rather rapidly to the posterior for the anterior 5 rings, whereafter the moderately deep axial furrows become subparallel. There are about 10 axial rings, of which the last few are rather indistinct, separated by rather broad (sag.) ring furrows. The anterior 3–4 rings retain spatulate distal terminations, while the anterior 4–5 ring furrows have prominent apodemal pits distally. The axis terminates in a bluntly rounded tip inside the pygidial margin so as to leave a short but distinct post-axial field. The pleural fields are subtrigonal, gently convex, each comprising 5 distinct pleurae that extend beyond the pygidial border to form prominent posteriorly directed lappets. The pleural grooves are broad and rather deep, tapering abaxially to become obsolete before the distal terminations of the pleurae are reached. The interpleural grooves are fine, tending to broaden and become more pronounced distally. There is an incompletely developed sixth pair of pleurae which does not develop lappets. The posterior margin of the pygidium is evenly rounded to slightly pointed between the fifth pair of lappets and is arched sagittally.

Discussion

In the interpretation of this species, and all the material discussed herein, the writer has been strongly governed by the consideration that a species is typified by the statistics of a population of individuals, not solely the characters of the holotype. Consequently, many of the trivial differences of previous workers are not herein considered of specific importance.

As noted by Rennie (1930), *Dalmanites (Eocorycephalus) capensis* (Fig. 33A) Reed was based upon damaged cephala of *Metacryphaeus caffer* of which it is, therefore, a synonym. Both Reed's (1925*a*) var. *albana*, said to have a more subquadrate glabella and to lack a median frontal process, and his *Dalmanites (Cryphaeus) caffer* var., based upon a pygidium distinguished by the more rapidly tapering axis and broader (sag.) post-axial field, are based upon characters of the individual that are not herein considered of taxonomic importance.

Dalmanites (Proboloides) ensifer Reed (Figs 33C, 64H) was based upon a unique cephalon that subsequently has generally been assigned to the genus *Schizostylus*. The writer has had the opportunity of studying this specimen; there seems little justification for interpreting the median frontal process as long as did Reed (1925*a*), and this is certainly a species of *Metacryphaeus*. It differs from *M. caffer* mainly in its state of preservation: it represents nodule preservation whereas most of the *M. caffer* material is preserved as dorsoventrally compressed internal moulds. It is only because of the different modes of preservation, reflecting perhaps different stratigraphic levels, that the writer is somewhat hesitant unequivocally to include *Dalmanites ensifer* in the synonymy of Salter's species.

The *Dalmanites (Cryphaeus)* cf. *rostratus* Kozlowski figured by Reed (1925*a*) (Fig. 70 herein) would appear to represent nothing more than a well-preserved frontal process such as might have been found on the holotype of *D. (Proboloides) ensifer*. Perhaps significantly, however, it is associated with *Bainella* and hence may represent a lower stratigraphic horizon than typical *M. caffer*. The true *Dalmanites rostratus* Kozlowski (1923: 44, pl. 5 (figs 1–9)) is the type species of the genus *Cryphaeoides* Delo (1935) and bears only a very superficial resemblance to *M. caffer*.

Dalmanites (Cryphaeus) cf. *pentlandi* Salter (Reed 1925*a*, pl. 11 (fig. 10)) (Fig. 67A herein) was said to differ from *M. caffer* in being rather coarsely and irregularly tuberculate. It seems probable, on account of the large size of this individual (sagittal length 71 mm excluding the cephalon), that the slight differences are due to a comparison of different ontogenetic stages.

Reed's (1925*a*: 145, pl. 11 (fig. 9)) *Dalmanites (Cryphaeus)* cf. *australis* Clarke was distinguished from *M. caffer* by its smaller eyes placed further to the anterior, its less inflated glabella and its more pointed genal angles. The writer has studies this specimen and is of the opinion that it is an individual of *M. caffer*. However, *M. australis* (Clarke) (1913: 110, pl. 4 (figs 1–5)) is indeed very close to *M. caffer* and, to judge from Clarke's perhaps idealized drawings, differs mainly in its relatively larger cheeks and the shape of the genal angles. It is noteworthy, however, that Clarke (1913: 114) wrote ' . . . the writer finds figure 4 of Salter's *Cryphaeus africanus* a true *Cryphaeus* tail and identical with *C. australis*; he believes that Salter's figure 1 belonged to the same animal and is *Cryphaeus australis*. . . . While the *Phacops africanus* rests well enough on Mr. Lake's type, let it be understood that *Cryphaeus australis* is present in the Bokkeveld fauna.' Clearly the taxonomic status of *M. australis* must await the modern revision of Clarke's material.

Metacryphaeus boulei (Kozlowski) (1923: 46, pl. 2 (fig. 15); Wolfart 1968: 88, pl. 11 (figs 1–3)) is a coarsely tuberculate species bearing a homoeomorphic resemblance to *Bainella arbuteus* (Lake), which is easily distinguished from *M. caffer*. *M. cornutus* Wolfart (1968: 95, pl. 12 (figs 2–5), pl. 13 (figs 1–4), pl. 14 (figs 1–2)) is readily separable from *M. caffer* in the possession of a long, cylindrical median spine to the occipital ring and a terminal spine to the pygidium.

Metacryphaeus venustus Wolfart (1968: 99, pl. 15 (figs 2–4), pl. 16, pl. 17 (figs 1–6)) is very close to *M. caffer* and perhaps especially to *M. australis*. It seems to differ from the South African species in its relatively longer (sag.) cephalon, with more strongly diverging axial furrows to the glabella, and its somewhat larger eyes that are not quite as close to the axial furrows as in *M. caffer*.

Fig. 62. A. *Metacryphaeus caffer* (Salter). The lectotype, BM–In28620, figured by Salter (1856, pl. 25 (fig. 11)). × 1.5. B. *Phacopina?* sp. BM–In28619, the original of Salter (1856, pl. 25 (fig. 10)), tentatively referred to *Phacopina lakei* (Reed) by Reed (1925*a*). Note the oval frontal lobe, distinct auxiliary impression system and relatively large eyes. × 3. Both preserved as internal moulds.

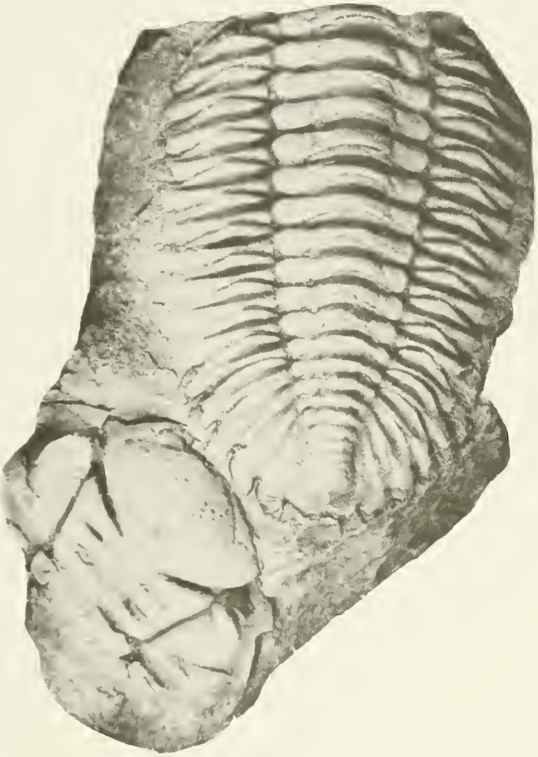

Fig. 63. *Metacryphaeus caffer* (Salter). An internal mould in the collection of R. Dick, Cape Town. × 1.

Metacryphaeus convexus (Ulrich) (1893: 16, pl. 1 (figs 9–11)) was based upon two isolated cephala and a pygidium drawn with an entire margin. As figured by Groth (1912, pl. 18 (fig. 4), pl. 19 (fig. 1)) and Wolfart (1968: 94, pl. 12 (fig. 1)), however, this species differs from *M. caffer* in having the sagittal area of the glabella, between the adaxial terminations of the glabellar furrows, strongly inflated and raised, with a tendency for the 2p furrows to be deepest abaxially and distinctly connected with the axial furrows.

Metacryphaeus dereimsi (Groth) (1912: 606, pl. 18 (figs 1–3)) was based upon isolated pygidia association with *M. convexus*. The post-axial field seems rather more triangular than is typical for *M. caffer* and thus this species closely approaches *M. venustus*. However, since most *Metacryphaeus* species have closely comparable pygidia, this name is probably best regarded as a *nomen dubium*.

Metacryphaeus praecursor Wolfart (1968: 82, pl. 8 (fig. 7)) was based upon an isolated cephalon which differs from *M. caffer* in having the 2p and 3p

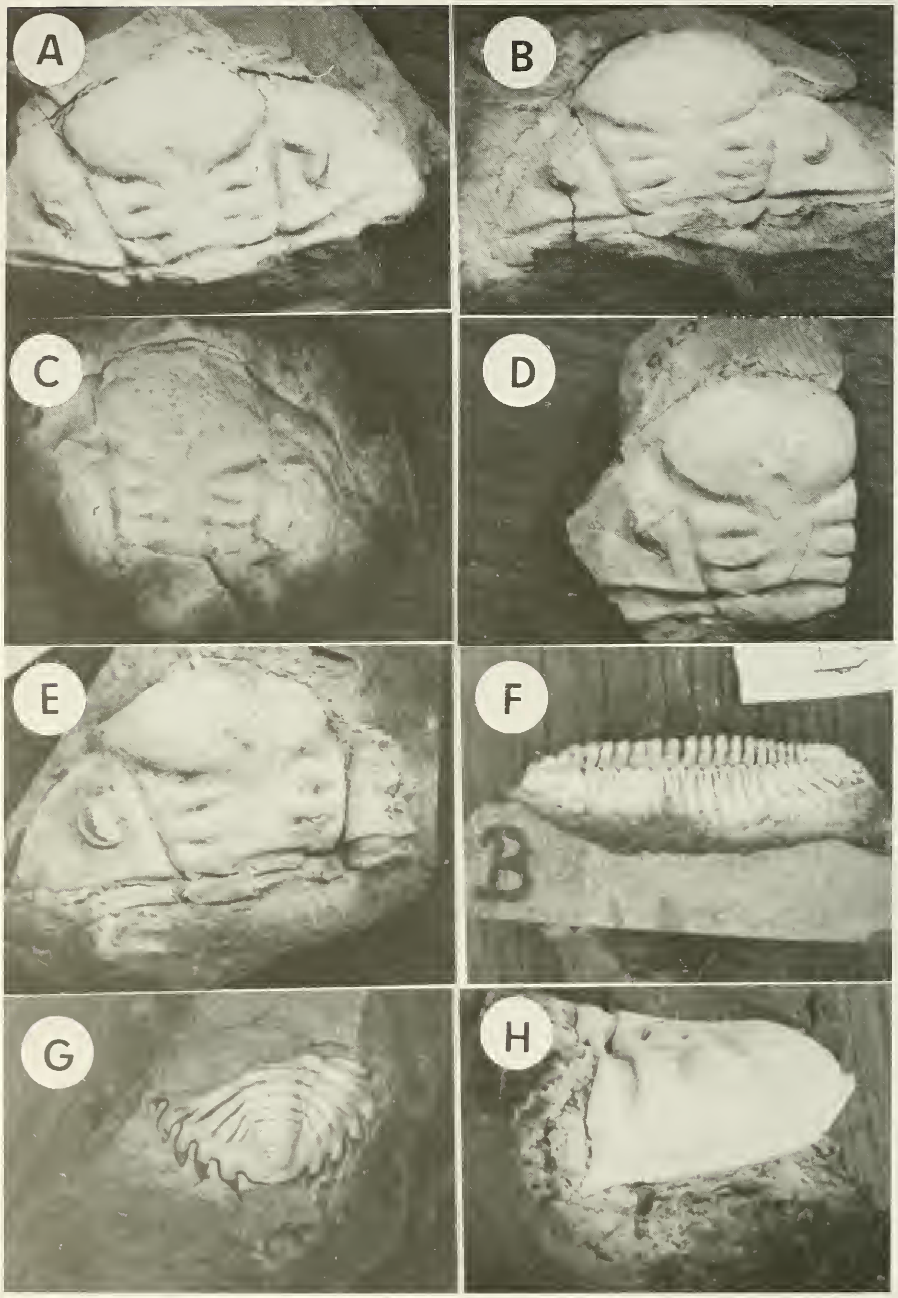

Fig. 64. *Metacryphaeus caffer* (Salter). A. SAM–PDB4335. B. SAM–PDB4352. C. SAM–PDB4340. D. SAM–PDB4075. E. SAM–PDB4363. F. SAM–PDB4354, in lateral view. G. SAM–PDB4329. H. SU–C2, the holotype of *Dalmanites (Proboloides) ensifer* Reed in lateral view. All preserved as internal moulds and all × 1,3.

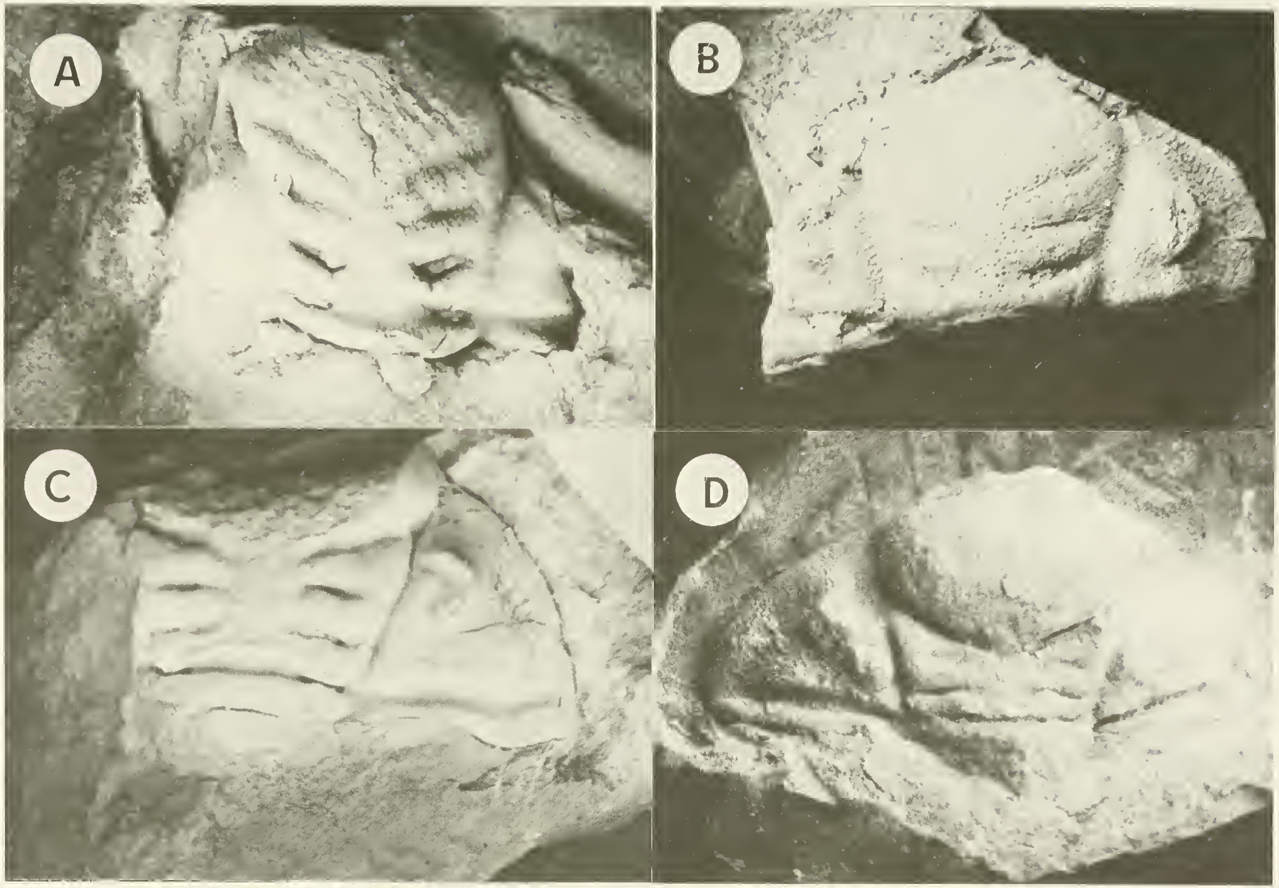

Fig. 65. A. *Bainella cristagalli* (Woodward). The original of Lake (1904, pl. 24 (fig. 3)), in the South African Museum. ×2. B. cf. *Kozlowskiaspis ceres* (Schwarz). SAM–7786, one of Reed's (1925*a*, pl. 9 (fig. 3)) figured syntypes of *Bainella baini* (Reed). Note the tuberculate frontal lobe that is well separated from the anterior ramus of the facial suture. ×1,9. C–D. *Metacryphaeus caffer* (Salter). C. SAM–PDB4037. ×1,4. D. SAM–7790, the original of Reed's 1925*a*, pl. 9 (fig. 10). ×1,6. All preserved as internal moulds.

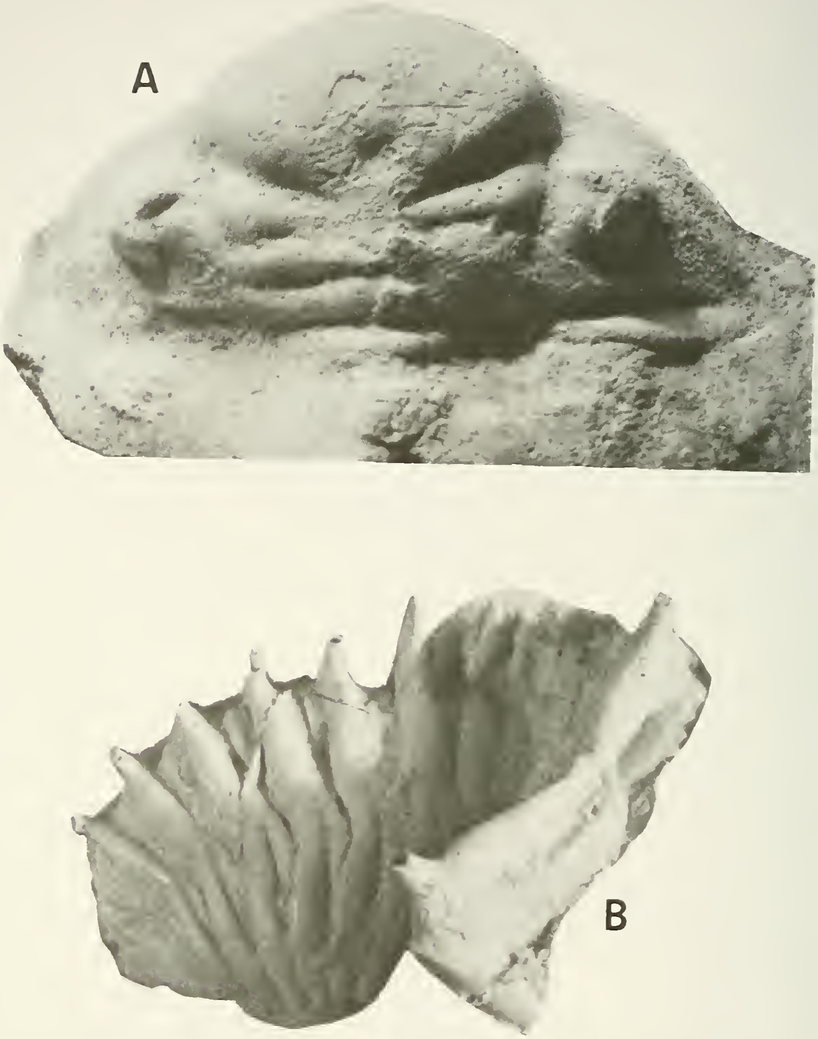

Fig. 66. A. *Metacryphaeus caffer* (Salter). AM–69, plaster cast of an external mould in nodule preservation. Note the weak ocular ridge. B. *Bainella africana* (Salter). Latex cast of the holotype of *Phacops acacia* Schwarz, AM–2124, preserved as an external mould, and figured by Schwarz (1906, pl. 10 (fig. 4)) and Rennie (1930, pl. 10 (fig. 5)). Note how both these workers misinterpreted the nature of the genal spines, which are situated inside (adaxial) of the genal angles and were almost certainly recurved distally. Both × 1.7.

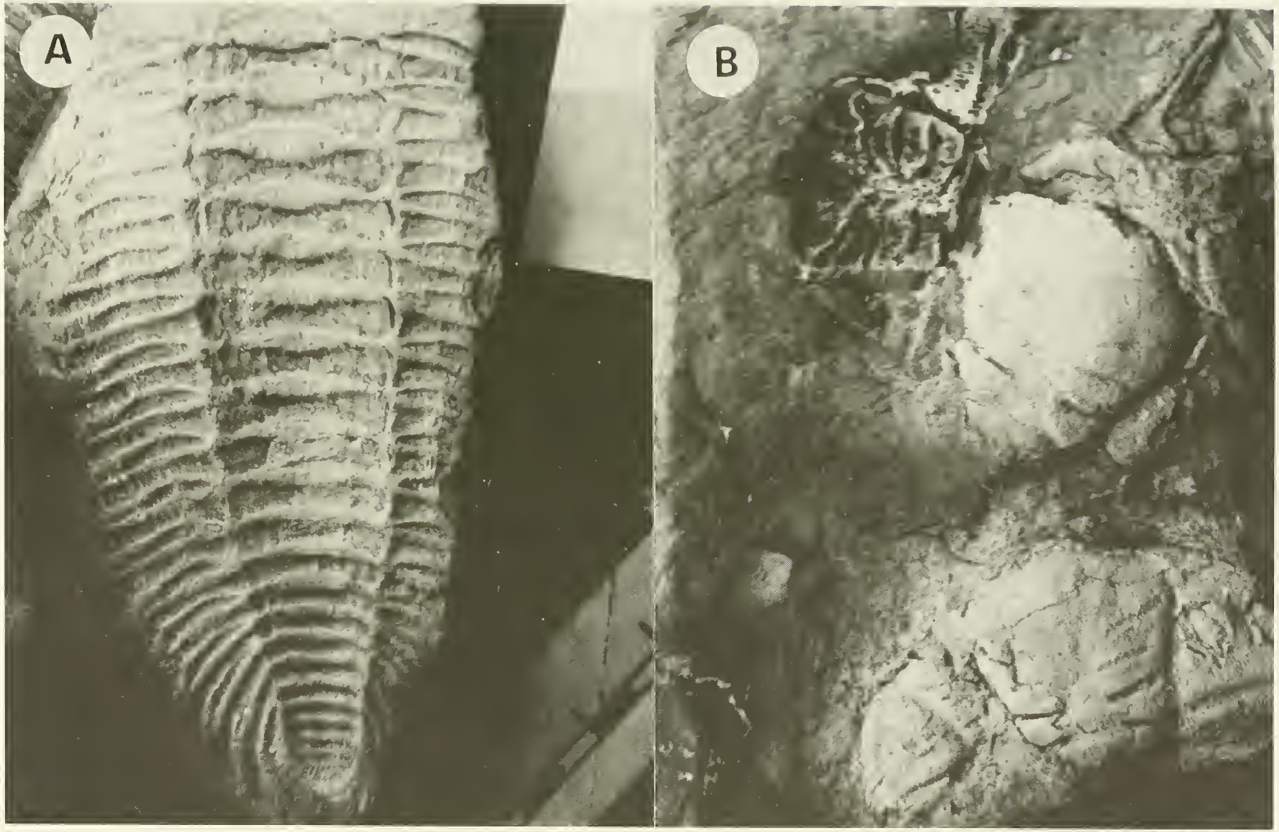

Fig. 67. A. *Metacryphaeus caffer* (Salter). SAM–2463, the external mould figured by Reed (1925*a*, pl. 11 (fig. 10)) as *Dalmanites (Cryphaeus)* cf. *pentlandi* Salter. × 1,5. B. *Bainella* cf. *africana* (Salter). SAM–7200, a group of cephala, preserved as internal moulds, forming part of Reed's extensive syntype series of *Bainella baini* (Reed), and the originals of his 1925*a*, pl. 9 (fig. 2). Preserved as internal moulds. × 1,5.

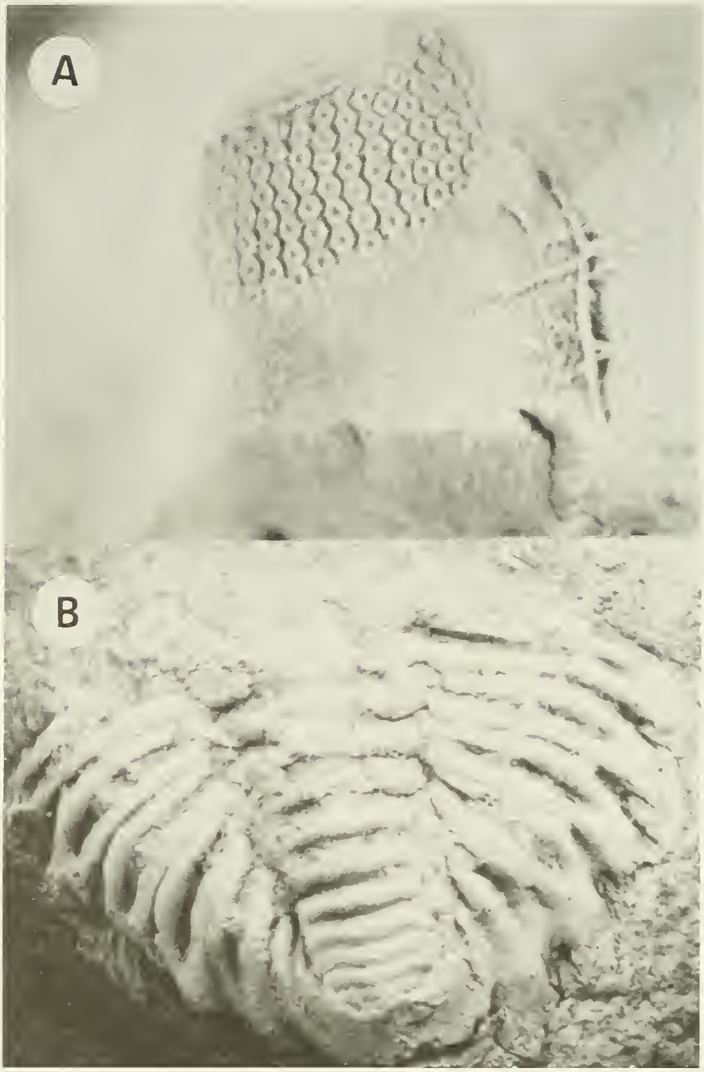

Fig. 68. A. *Bainella africana* (Salter). RO–708, showing the visual surface of the eye. Much enlarged. B. *Metacryphaeus caffer* (Salter). SAM–PDB4341. × 1,8. Both preserved as internal moulds.

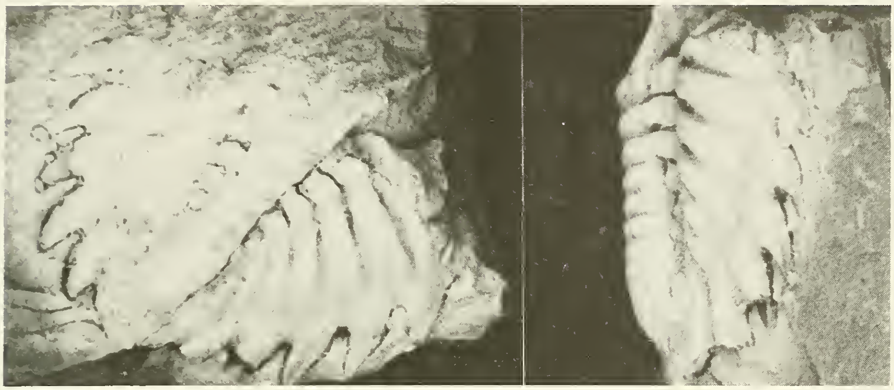

Fig. 69. *Metacryphaeus caffer* (Salter), SAM–PDB3943, preserved as an internal mould. × 2.

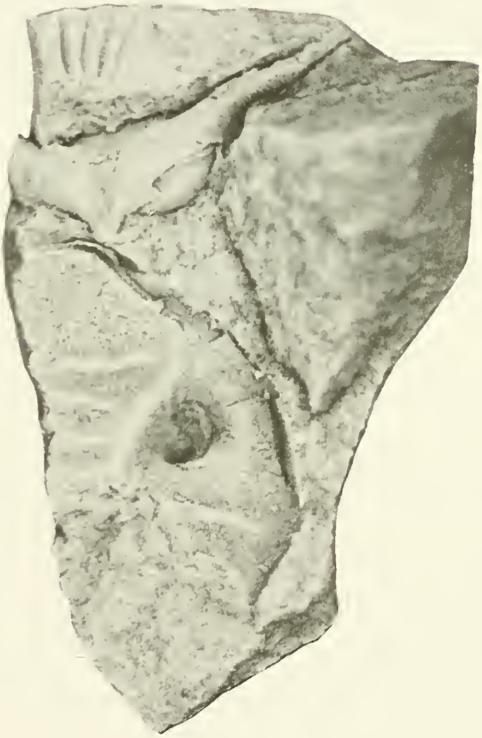

Fig. 70. Aff. *Metacryphaeus caffer* (Salter). SMC–A3063, the rostral fragment figured by Reed (1925*a*, pl. 8 (fig. 2)) as *D. (Cryphaeus)* cf. *rostratus* Kozlowski, associated with a cephalon of *Bainella* '*baini*' (Reed). Both preserved as internal moulds. × 2.

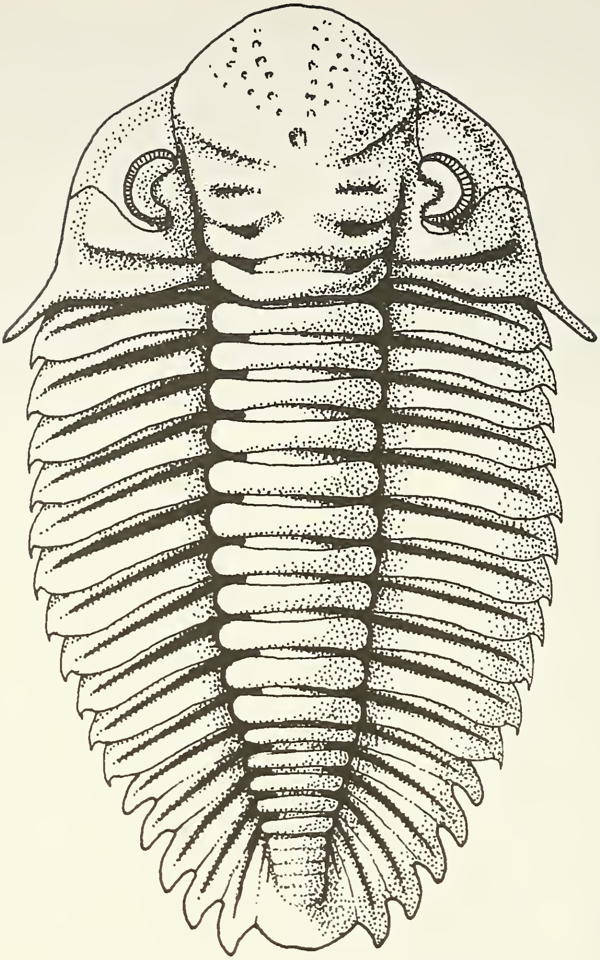

Fig. 71. *Metacryphaeus giganteus* (Ulrich).
A reconstruction based upon the figured material of Wolfart (1968).
× 1,8.

glabellar lobes rather inflated, with the L1 lobes narrow and reduced. *M. curvioculatus* (Wolfart) (1968: 76, pl. 6 (fig. 2)) is very close to *M. venustus* and differs from *M. caffer* in much the same respects as the latter species.

Metacryphaeus giganteus (Ulrich) (1892: 14, pl. 1 (figs 6–8)) (Fig. 71 herein) is very close to *M. caffer*, at least some of the differences relating to the nodule preservation of the Bolivian material. However, it may be distinguished from the South African species by its more rounded frontal lobe and in the development of seemingly true genal spines. Its occipital furrow also appears to be relatively broader (sag.).

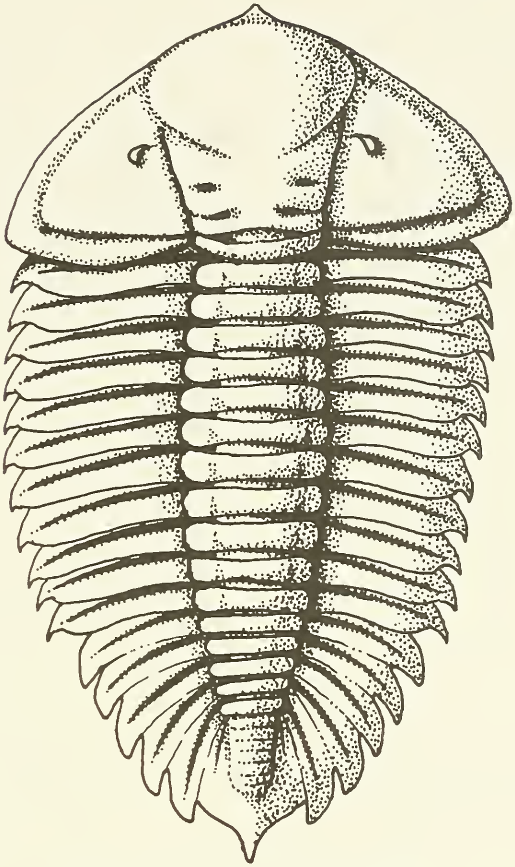

Fig. 72. *Punillaspis argentina* (Baldis).
A reconstruction based upon the figured material.
×2.

Metacryphaeus tuberculatus (Kozlowski) (1923: 43, pl. 3 (figs 20–21)) was originally described as a variety of *M. australis* (Clarke) but elevated to specific status by Wolfart (1968). As figured by Kozlowski (1923), the cephalon is indistinguishable from *M. caffer*, while the pygidium merely differs in its slightly more triangular outline (an artefact of nodule preservation?). The cephala figured by Wolfart (1968: 102, pl. 17 (fig. 7), pl. 18 (fig. 1)) cannot satisfactorily be separated from *M. caffer* and should probably be regarded as conspecific. However, since N. Eldredge of the American Museum of Natural History is currently revising the Bolivian calmoniids, the taxonomic position of this species should await his conclusions.

Metacryphaeus argentina Baldis (1967: 792, pl. 1 (figs 7–11), pl. 2 (figs 1–6)) (Fig. 72 herein) is a curious species whose very reduced, minute eyes readily distinguish it from *M. caffer* and, indeed, all other species of *Metacry-*

phaeus. It was recently (Baldis & Longobucco 1977*a*) made the type of the new genus *Punillaspis*.

Occurrence

Metacryphaeus caffer (Salter) is abundant in the Voorstehoek Formation of the Bokkeveld Group, and the probably conspecific *M. tuberculatus* (Kozlowski) ranges from the upper part of the Belen Formation into the Sicasica Formation of Eifelian age in Bolivia. There is definitely a *Metacryphaeus* species present in the Gydo Formation but none of the material available to the writer has been sufficient to identify *M. caffer* positively; it could be *M. giganteus* (Ulrich) to judge by the stratigraphic relationships of the various species of *Metacryphaeus* in Bolivia.

Metacryphaeus (Metacryphaeus) venustus Wolfart, 1968

Figs 73–75, 76A, C–D, 77C–D, F, 78B–C

Cryphaeus australis Clarke, Kozlowski, 1923: 41, pl. 3 (figs 3–6, 8, 14–17). Reed, 1925*a*: 139 (*pars*). Fricke *et al*., 1964: 15–16.
Metacryphaeus australis (Clarke) Braniša, 1960: 68, 74.
Metacryphaeus caffer (Reed) Braniša, 1960: 66, 71; 1965: 106, pl. 21 (figs 10–15). Fricke *et al*., 1964: 16.
Metacryphaeus venustus Wolfart, 1968: 99, pl. 15 (figs 2–4), pl. 16, pl. 17 (figs 1–6). Eldredge & Ormiston, 1979: 160.

Material

Fourteen specimens, PRV–716, 718–719, 721, 724, 729, 731–734, 777, 780, 791, and 796, all preserved as internal moulds, and all from the Waboomberg Formation at Klein Tafelberg.

Description

Cephalon. The cephalon is semicircular, much broader (trans.) than long (sag.), with the cephalon diverging strongly to the anterior. The frontal lobe is subrhomboidal, with a prominent posterior median impression and no distinct auxiliary impression system. The 3p furrows are deep, directed posteromedially, and distinctly connected to the well-developed axial furrows. The 2p furrows are deep, transverse, and connected to the axial furrows, while the 1p furrows are very deep, anteriorly concave, and also distinctly connected to the axial furrows. The occipital furrow is arched forward sagittally and with deep apodemal pits distally. The L1 lobes are very narrow (exsag.), anteriorly concave, and in some individuals give the impression of being weakly connected across the glabella (Fig. 76A, C). The L2 lobes are more or less of constant width, and the L3 lobes broaden (exsag.) distally. The median glabellar region, between the adaxial terminations of the L2 and L3 lobes, seems to be slightly raised in some individuals (Fig. 77C). The occipital furrow is arched forward sagittally, and with deep apodemal pits distally. The occipital ring is of constant width (exsag.) and lacks tuberculation. There is a narrow

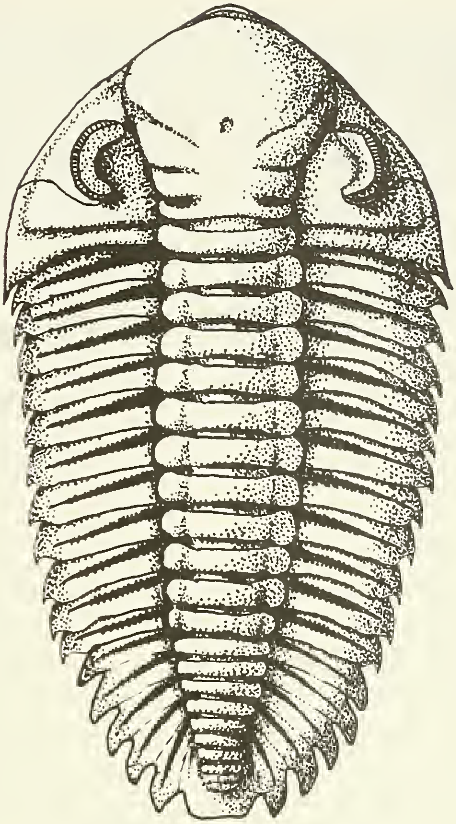

Fig. 73. *Metacryphaeus venustus* Wolfart.
A reconstruction based upon the material from
the Waboomberg Formation. × 2.

anterior border that, in some of the better preserved cephala (Fig. 76A), shows the hint of a very short, median rostrum.

The cheeks are subtrigonal and curved strongly downward distally. The posterior border furrows are deep, transverse, whereas the lateral border furrows are shallow and indistinct. The posterior border broadens (exsag.) rather markedly towards the genal angles. In PRV–796 (Fig. 75), the genal angles are produced posteriorly, with a rather distinct spinule. The eyes are large, about 40 per cent of the exsagittal cephalic length, and comprise subvertical rows of ocelli, with 6–7 lenses in the middle row. In PVR–796 only about 18 rows of ocelli could be counted. The anterior branch of the facial suture is not clearly visible in any of the available material; presumably it was in close juxtaposition with the glabellar frontal lobe. The posterior suture curves strongly forward after leaving the eye, and then recurves to meet the lateral border approximately opposite the posterior margin of the eye.

Fig. 74. *Metacryphaeus venustus* Wolfart. PRV–791, preserved as an internal mould. × 2.

Thorax. There is little to separate the thorax of *Metacryphaeus venustus* from that of *M. caffer*, and hence it does not merit redescription.

Pygidium. The pygidium is wider (trans.) than long (sag.), with a convex axis that tapers strongly to the posterior for the first 5 rings, whereafter the distinct axial furrows become subparallel. After the eighth axial ring the segmentation becomes indistinct but there may have been as many as 11 rings; certainly in some individuals 10 can be counted. The anterior 4 ring furrows have apodemal pits distally and the axis is bluntly terminated to the posterior, leaving a very pronounced post-axial field. The pleural fields are subtrigonal

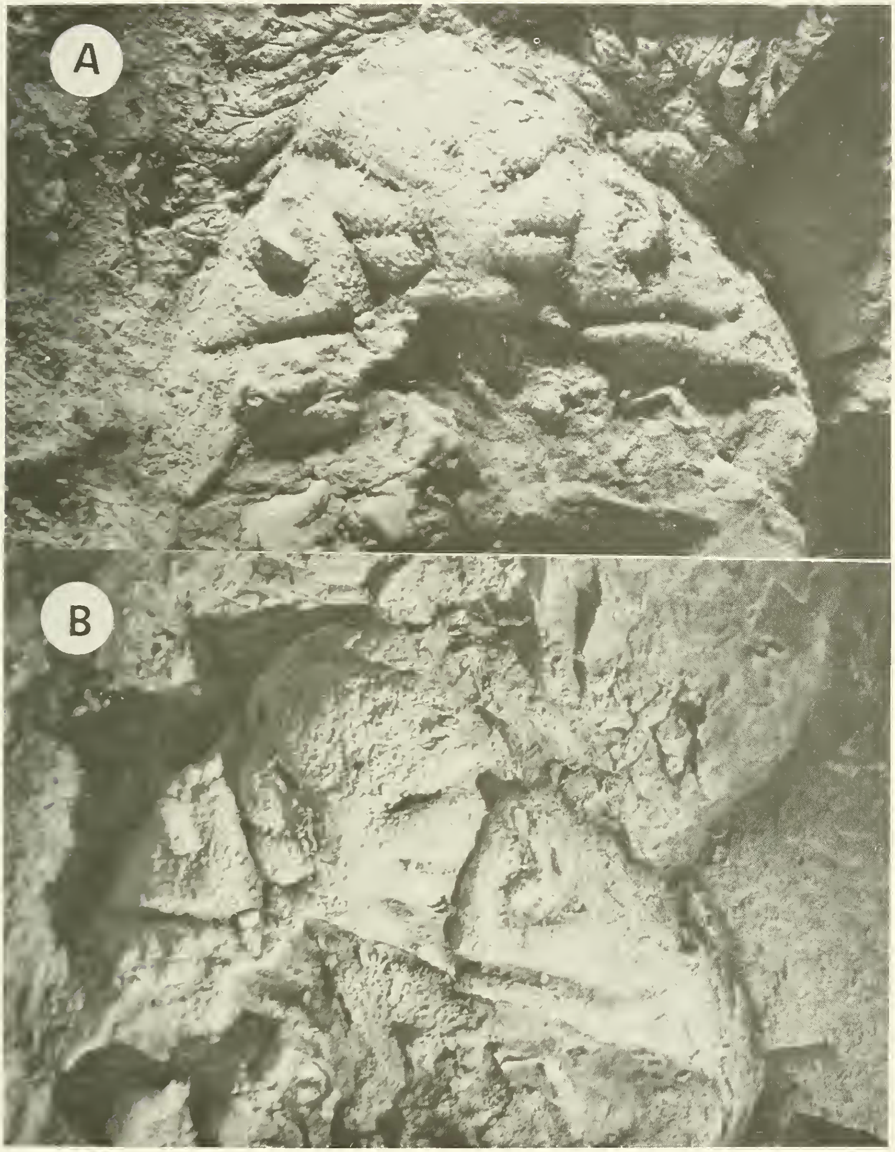

Fig. 75. *Metacryphaeus venustus* Wolfart. PRV–796, preserved as an internal mould. Note the very reduced L1 lobes, large eyes, and distinct spines to the genal angles. × 3.

and rather strongly convex. There are 6 distinct pleurae, each with a pronounced pleural groove and faint interpleural furrows, with a very reduced seventh to the posterior. The anterior 5 pairs of pleurae terminate in prominent lappets distally. In PRV–724 there are weak, oblique tubercles, on the anterior moiety of each pleura (Fig. 78B), marking the fulcrum. This feature is not, however, persistent and its taxonomic significance is uncertain. The post-axial field is relatively rather broad, about 22 per cent of the sagittal length of the pygidium, and appears to be abruptly truncate to the posterior (Fig. 78C).

Discussion

The Bokkeveld material shows a few minor points of differences when compared with the Bolivian material. These include apparently fewer lenses to the eyes and the presence in at least one individual of weak tubercles marking the fulcral axis of the pygidium. In view of the remaining marked similarities between the two forms, however, the differences are not at present considered of taxonomic importance. Differences from the other species of *Metacryphaeus* are discussed under *M. caffer*.

Occurrence

Metacryphaeus venustus Wolfart is currently known only from the upper part of the Belen Formation and the Sicasica Formation of Bolivia, and the Waboomberg Formation of South Africa.

Metacryphaeus (Metacryphaeus?) cf. *koukharskii* (Baldis & Longobucco, 1977)

Figs 76B, 77A–B, 79

Compare

Acastoides koukharskii Baldis & Longobucco, 1977*b*: 171, figs 1–3.

Material

Two specimens PRV–175 and 428, both preserved as internal moulds, the latter from the farm Bon Chretien, 15 km due east of Ceres, south-western Cape.

Description

Cephalon. The cephalon is subtrigonal in outline and rather convex, with strongly downturned cheeks. The axial furrows are pronounced and diverge anteriorly. The glabella is convex, with a somewhat inflated frontal lobe that is oval in shape and without a distinct auxiliary impression system. The 3p furrows are weakly impressed, straight, and directed anterolaterally to connect with the axial furrows. The 2p furrows are moderately impressed, transverse, anteriorly convex, and distally connected with the axial furrows. The 1p furrows are very deep, transverse, and strongly connected to the axial furrows.

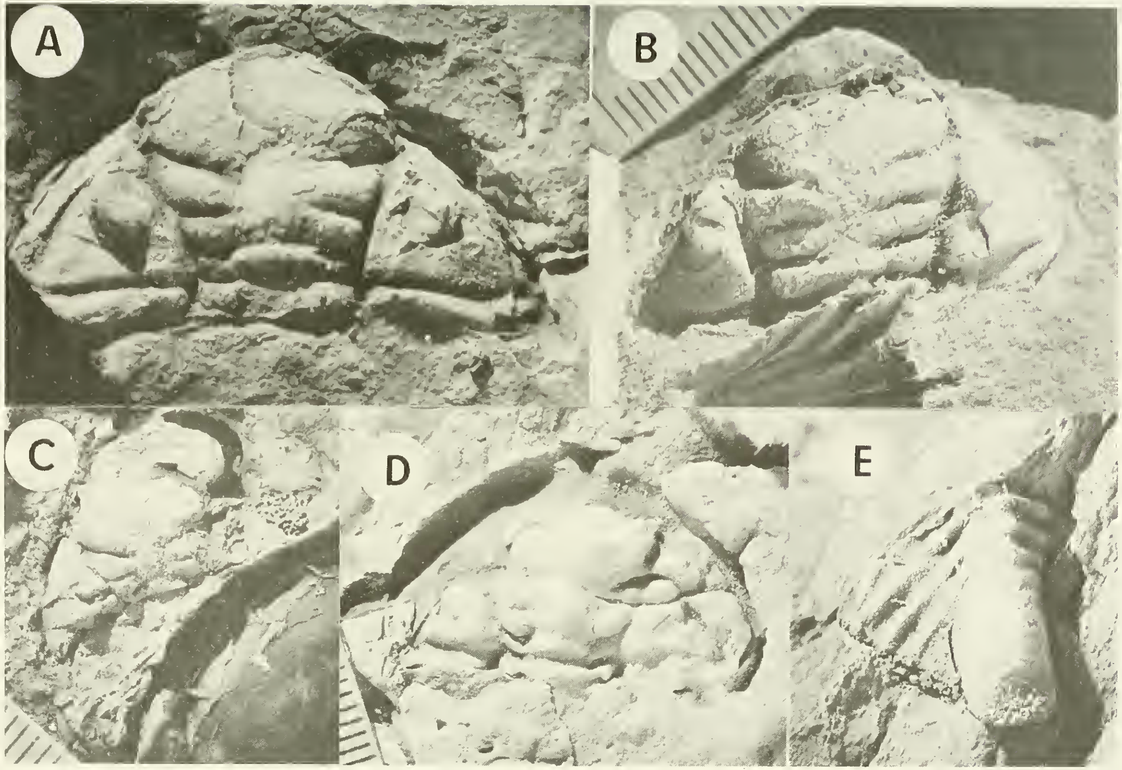

Fig. 76. A, C–D. *Metacryphaeus venustus* Wolfart. A. PRV–780. Note how the 1p furrows are proximally connected by a distinct transglabellar furrow. ×3,5. C. PRV–732. ×2. D. PRV–777. ×2. B. *Metacryphaeus* cf. *koukharskii* (Baldis & Longobucco). PRV–175. ×2. E. *Bainella africana* (Salter). PRV–92, a typical pygidium. ×2. All preserved as internal moulds.

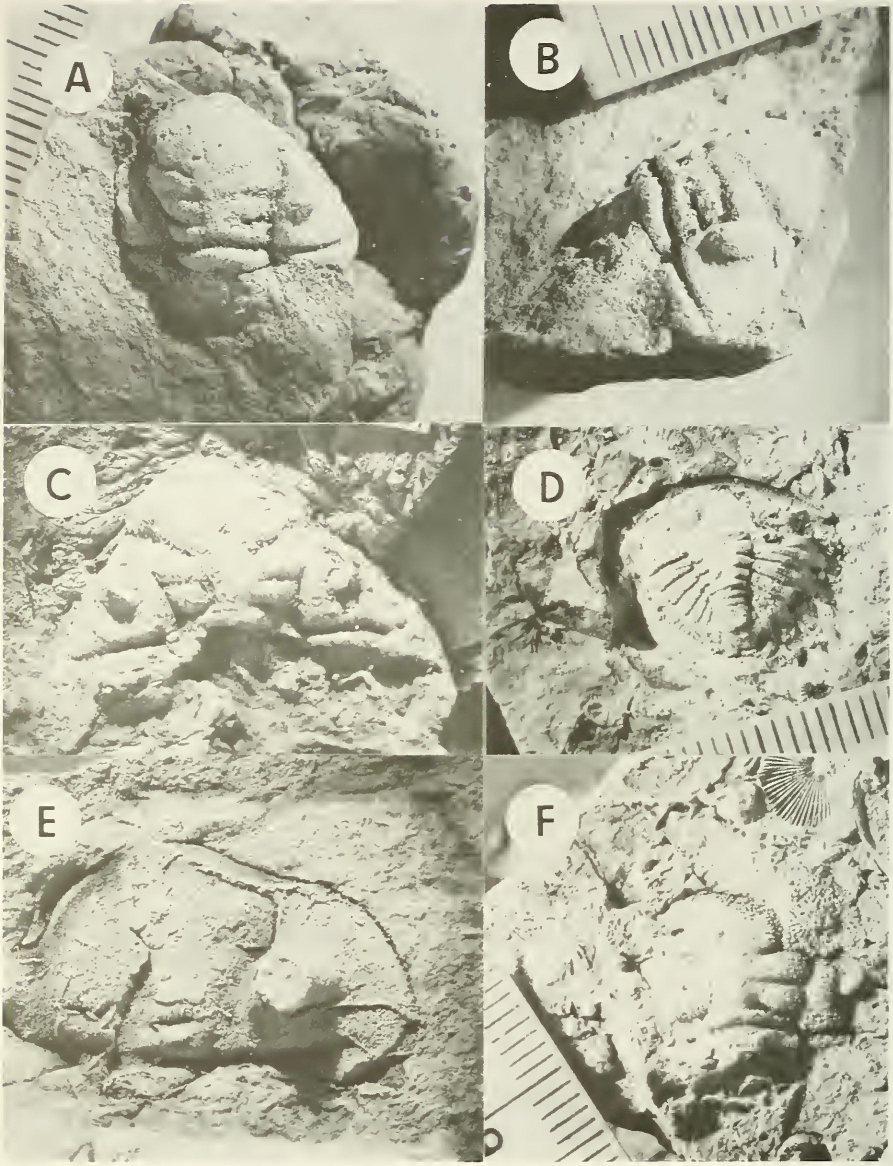

Fig. 77. A–B. *Metacryphaeus* cf. *koukharskii* (Baldis & Longobucco). PRV–428. Note the abaxial taper of the L2 lobes and the connection of the 2p furrows with the axial furrows. C–D, F. *Metacryphaeus venustus* Wolfart. C. PRV–796. Note the very reduced L1 lobes. D. PRV–729. F. PRV–733. E. *Bainella africana* (Salter). PRV–57. All preserved as internal moulds and all × 2.

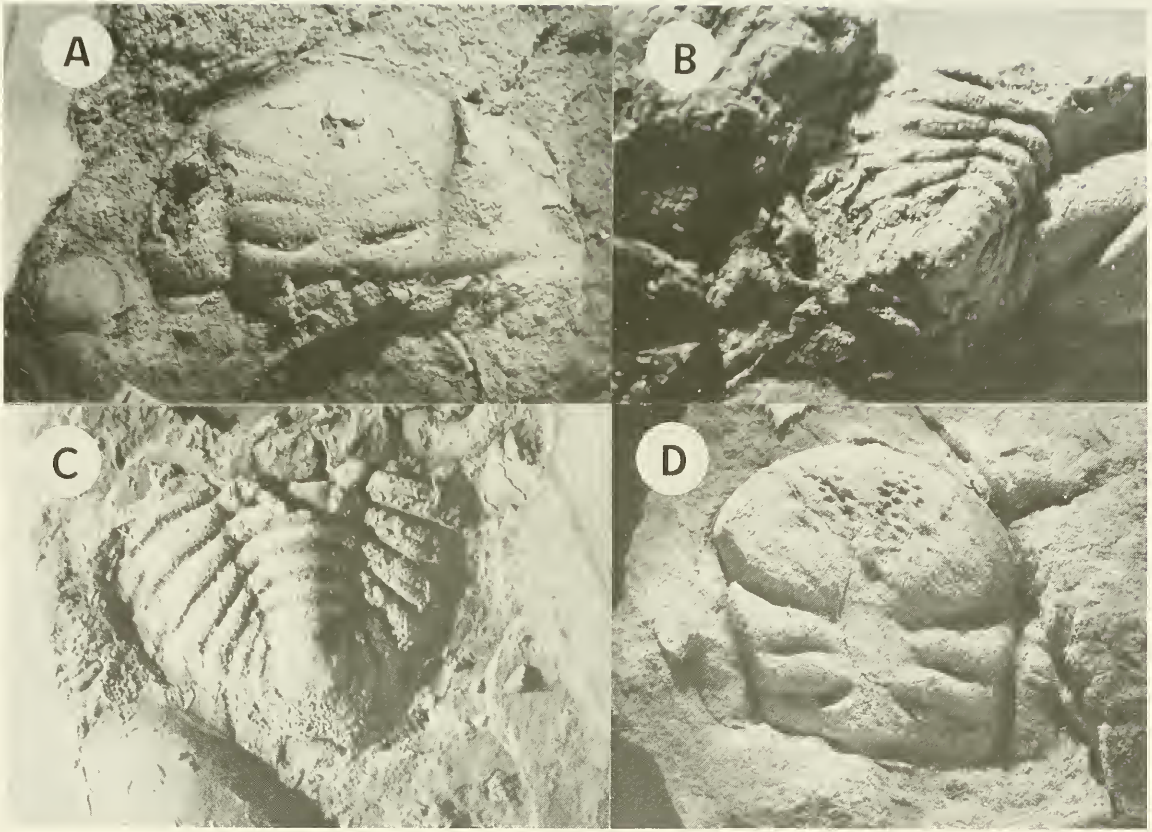

Fig. 78. A. *Bainella africana* (Salter). PRV–3197, one of the syntypes of *B.* '*baini*' (Reed). B–C. *Metacryphaeus venustus* Wolfart. B. PRV–724. Note the elongate, oblique tubercles at the fulcral axis. C. PRV–718. An example lacking fulcral tubercles. × 3. D. *Metacryphaeus caffer* (Salter). PRV–922, showing a well-developed auxiliary impression system. All preserved as internal moulds and all × 2 unless otherwise stated.

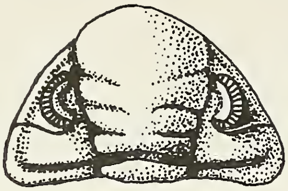

Fig. 79. *Metacryphaeus* cf. *koukharskii* (Baldis & Longobucco). A reconstruction based upon PRV–428. ×2.

The L1 lobes are moderately broad (exsag.) and of more or less constant width, and the L2 lobes characteristically narrow abaxially. There is no posterior median depression to the frontal lobe. The occipital furrow is deep, anteriorly convex, of constant width, and with deep apodemal pits distally. The occipital ring is smooth and of approximately constant width (exsag.). The cheeks are subtrigonal in outline, strongly downturned, and with deep, transverse posterior border furrows. The lateral border furrows are poorly developed and, although not preserved, the genal angles give the impression of having been subrounded. The eyes are moderately large, about 50 per cent of the exsagittal length of the cephalon, and situated opposite the L2 and L3 lobes. The anterior ramus of the facial suture could not be discerned, but the posterior branch meets the lateral border opposite the posterior margin of the eye.

Discussion

The Bokkeveld example closely resembles the holotype of Baldis & Longobucco (1977*b*), from which it seemingly differs only in being more strongly convex and with more sharply down-turned cheeks. These features may, however, be artefacts of preservation and, allowing for a moderate range of intraspecific variation, the Bokkeveld example may reasonably be compared with the Argentine species.

The generic assignment of '*Acastoides*' *koukharskii* is difficult; it does not belong to the Boreal *Acastoides*, which differs in having weakly impressed 2p furrows that do not connect with the axial furrows, and with very reduced L1 lobes. In both *Pennaia* and *Phacopina* the 2p furrows typically become obsolete distally, with the fusion of the L2 and L3 lobes. It thus finds its closest ally in *Metacryphaeus venustus* Wolfart, a somewhat atypical *Metacryphaeus* in the strongly reduced nature of its L1 lobes and the distinct connection of the 2p furrows with the axial furrows. None the less, assignment of '*A*'. *koukharskii* to the genus *Metacryphaeus* seems reasonable.

Occurrence

Metacryphaeus koukharskii (Baldis & Longobucco) is currently recorded from an uncertain level in Argentina, but may also be present in the Bokkeveld sequence of South Africa.

Genus *Typhloniscus* Salter, 1856

Type species *Typhloniscus baini* Salter, 1856; by monotypy

Typhloniscus baini Salter, 1856

Figs 7B, 33E–F, 39C, 41B–C, 50E, 80–82

Typhloniscus baini Salter, 1856: 221, pl. 25 (fig. 14). Lake, 1904: 213, pl. 25 (figs 8–9). Clarke, 1913: 158. Reed, 1925*a*: 162; 1927: 347. Rennie, 1930: 355, pl. 10 (figs 6–12). Struve (*in* Harrington *et al.*), 1959: 0487, fig. 385,1.
Acaste (Typhloniscus) baini (Salter) Kozlowski, 1923: 31.
Acidaspis atherstonei Reed, 1925*a*: 188, pl. 7 (fig. 7).
Acidaspis capensis Reed, 1925*a*: 189, pl. 11 (figs 6–7).

Material

The holotype, by monotypy, BM–28635, together with BM–In24103–4, SU–K463, SAM–7186, 7799, 8978, 8982–8983, PRV–624–625, AM–2561, and RO–3, 702, 753–754, 757, 782, 793–794, 796, and P3.

Description

Cephalon. The cephalon is subpentagonal in outline and more than twice as wide as the sagittal length. The glabella is pentagonal in outline, weakly convex, and with straight axial furrows that diverge slightly to the anterior. On internal moulds the axial furrows are very deep (Fig. 81), whereas where the cuticle is preserved (Fig. 33F) they are broad and shallow. The 3p glabellar furrows are moderately deep, directed posteromedially at about 45° to the axial furrows and weakly connect to the axial furrows. On internal moulds the 2p furrows are straight, directed posteromedially at about 60° to the axial furrows, weakly connected to the axial furrows, and with very deep adaxial apodemal pits. The 1p furrows are parallel to and similar in all respect to the 2p furrows. On internal moulds the occipital furrow is broadest sagittally, but where the cuticle is preserved it is of uniform width and with distal apodemal pits. The occipital ring is of uniform width on internal moulds, but where the cuticle is preserved is biconvex and several times broader than the occipital furrow sagittally. Curiously, the deep posterior border furrows of the cheeks do not connect with the occipital furrow due to narrow branches of the occipital ring that connect in this position. The posterior border furrows are well developed and deep, but the lateral border furrows are broad, shallow and indistinct. The posterior borders broaden rapidly towards the genal angles that are produced backward and sharply rounded. The genae, which are entirely on the fixigenae, are raised and strongly convex, with scattered pits on the internal mould but a coarsely granulose cuticle. Eyes are apparently lacking but there are small ridges at the extreme anterior of the cheeks, opposite the distal terminations of the 3p furrows, which are separated from the cheek area by shallow grooves. They may represent relict ocular ridges. There is a very narrow anterior border with the vaguest hint of a median frontal process. The facial suture runs along the dorsal surface of the anterior border and becomes inframarginal opposite the 'eye ridges'.

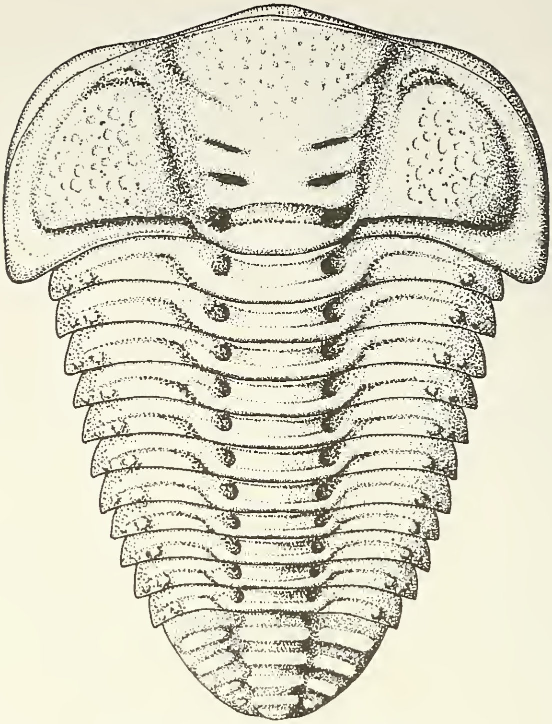

Fig. 80. *Typhloniscus baini* Salter.
A reconstruction based upon the available material.
×2.

Thorax. The thorax tapers rather rapidly to the posterior, as does the axis which is about one-third the thoracic width. The axial rings are thickest along their posterior borders and separated by much wider ring furrows, with deep apodemal pits distally. The pleurae have moderately well-developed pleural grooves and distinct interpleural furrows. The posterior moiety of each pleura broadens (exsag.) and thickens distally and, after the fulcrum, bears 1–3 tiny tubercles, well shown by PRV–624. The pleurae have pointed distal terminations and, where the cuticle is preserved, are coarsely granulose.

Pygidium. The pygidium is small, micropygous, with an almost semicircular outline. It is somewhat wider than the sagittal length and with an entire margin. The axis is very prominent, cylindrical, and tapers only very slightly to the posterior. It comprises 4 prominent rings, slightly wider than the ring furrows, the anterior three of which preserve apodemal pits. A variably developed fifth ring is pronounced on some individuals but very reduced and insignificant in others. The axis increases in height posteriorly and has a bluntly rounded terminal end which tends to overhang the pygidial margin. The pleural fields comprise 3 pairs of very prominent, raised ribs that increase in height

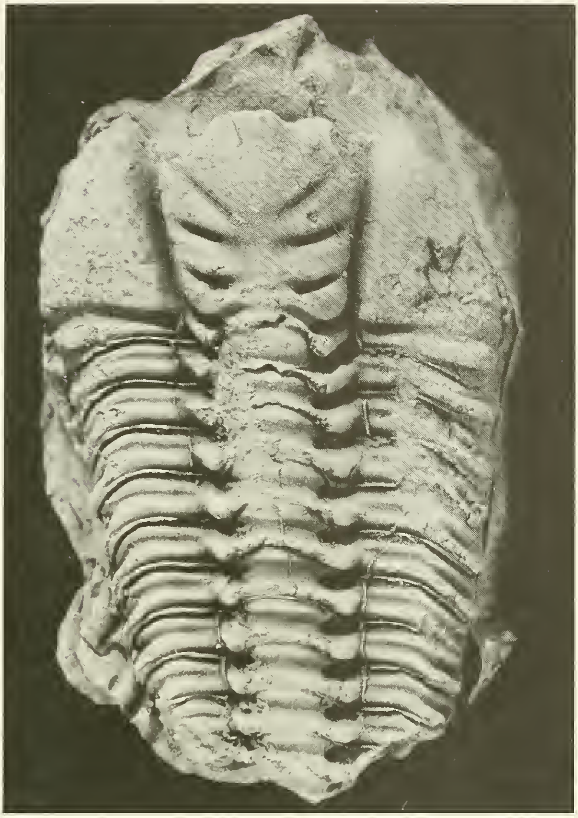

Fig. 81. *Typhloniscus baini* Salter. The holotype and original of Salter (1856, pl. 25 (fig. 14)), preserved as an internal mould; housed in the British Museum (Natural History). × 2.

distally and are separated by slightly narrower, deep interpleural grooves. The pleural furrows seem to be obsolete. A fourth very reduced pair of pleural ribs is generally present.

Discussion

The writer has had the opportunity of studying the holotypes of both *Acidaspis atherstonei* Reed, BM–In24103, and *A. capensis*, SAM–7799, and it is clear that both species are based upon isolated thoraxes of *Typhloniscus baini*. Except for some species of the homoeomorphic Ordovician genus *Placoparia* and '*Typhloniscus*' *princeps* Reed (1908: 433, pl. 14 (figs 1–3)), (a *Cheirurus?*), there are no species with which the present form warrants comparison.

Occurrence

Typhloniscus baini Salter is currently known only from the Gydo Formation of the Bokkeveld sequence.

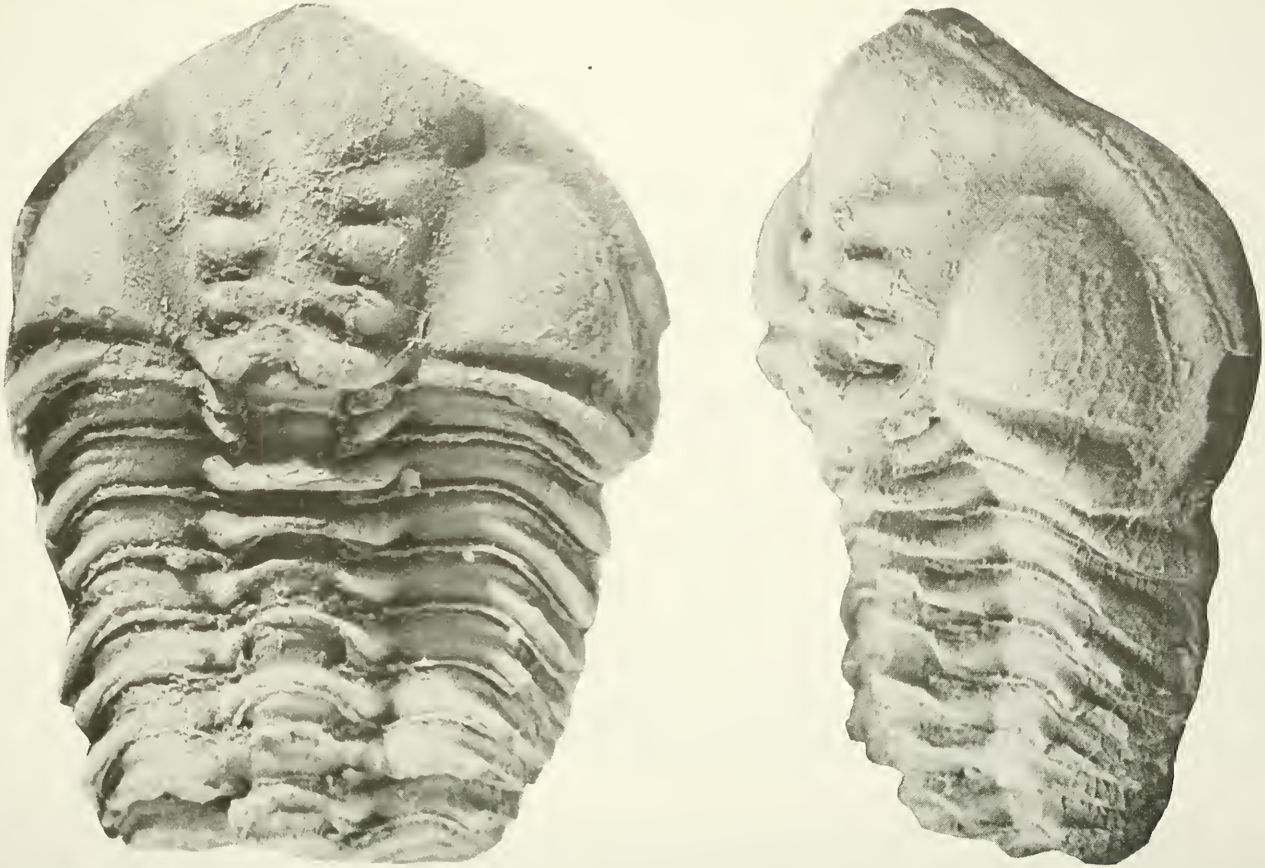

Fig. 82. *Typhloniscus baini* Salter. PRV–624. Note the 'eye ridges' and the distinct tubercles to the posterior moieties of the thoracic pleurae. × 2,6.

Genus *Phacopina* Clarke, 1913

Type species *Phacops braziliensis* Clarke, 1890;
by original designation

Discussion

The writer is, at present, unhappy with the treatment of this genus by Eldredge & Braniša (1980). These authors would regard *Jujuyops*, type species *J. nonoctubrensis* Baldis, Benedetto, Blasco & Martel (1976, pl. 5 (figs 1–4)), as a junior subjective synonym of *Phacopina*, noting that their *Phacopina convexa* may be conspecific with *J. nonoctubrensis*. However, *P. convexa* Eldredge & Braniša differs markedly from *P. braziliensis* in having much smaller eyes (27–34 % of the exsaggital cephalic length as against almost 50 %, to judge from Eldredge & Braniša's illustrations) that are situated far forward (39 % of the exsagittal cephalic length from the posterior margin of the cephalon to the posterior limit of the eye, whereas the eyes of *P. braziliensis* almost touch the posterior border furrows). Moreover, the glabellar segmentation of *Jujuyops* is more pronounced with transversely longer 1p furrows, its axial furrows are subparallel and do not diverge strongly towards the anterior as in *P. braziliensis*, and its L1 lobes are much broader exsagittally (14 % of the sagittal length of the glabella as against only 8,3 % in *P. braziliensis*). To judge from other calmoniid trilobites, these differences warrant, in the writer's opinion, generic separation. Since N. Eldredge is currently revising Clarke's Brazilian material, further comment must await the appearance of his work and the South African material is referred to the oldest available name, *Phacopina*.

Phacopina hexensis (Reed, 1925)

Fig. 83

Proetus hexensis Reed, 1925*a*: 121, pl. 7 (fig. 8).

Material

Reed's two syntype pygidia, SU–H176 and SAM–3889, of which the former is herein selected as lectotype.

Description

This species is based upon pygidia and the characters of the cephalon and thorax are currently unknown. The lectotype is moderately convex, semicircular in outline, and with an entire margin. The axis is broad anteriorly but tapers rapidly to the posterior to terminate in a bluntly rounded tip short of the posterior margin so as to leave a distinct post-axial field. On the lectotype, only the first two axial rings, separated by narrow ring furrows, are reasonably distinct, as well as the first two pairs of pleural grooves. The remaining segmentation is very indistinct to obsolete. The pleural grooves do not reach the pygidial margins, so that there is a smooth border strip. The surface of the pygidium is very finely granulose, the lectotype retaining much of the cuticle.

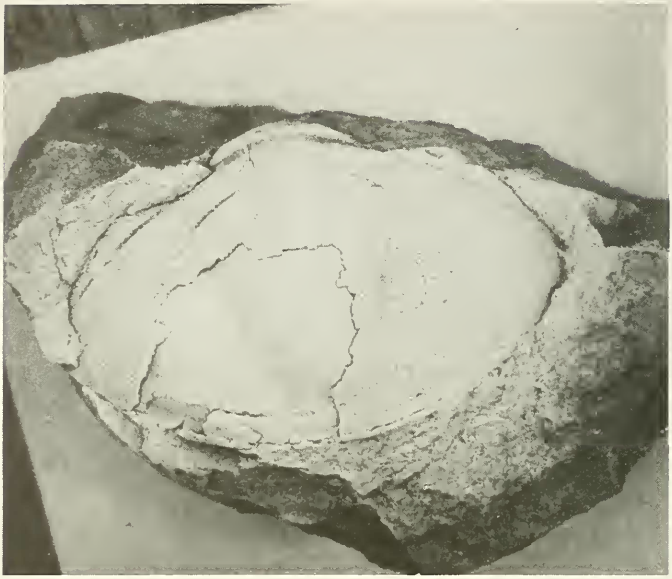

Fig. 83. *Phacopina hexensis* (Reed). SU–H176, the lectotype and original of Reed's 1925*a*, pl. 7 (fig. 8) which retains much of the cuticle. ×2,5

Discussion

The lectotype pygidium of *Phacopina hexensis* is virtually identical to that of *P. convexa* Eldredge & Branišа (1980, fig. 22K) (Fig. 84 herein) and also to that of *Andinacaste chojnacotensis* (Swartz) (1925: 50, pl. 1 (figs 8–10); Wolfart 1968: 122, pl. 23 (figs 4–6), pl. 24 (figs 1–4)). Complete examples of the South African species are required, however, before it can be usefully compared with the South American material.

Occurrence

Phacopina hexensis (Reed) is currently a South African endemic from an uncertain level in the Bokkeveld sequence.

Phacopina lakei (Reed, 1925)

Figs 59A, 85A–B, D, 86–87A, C–D, 88

Phacops (Calmonia) lakei Reed, 1925*a*: 154, pl. 9 (figs 4–5).

Material

The holotype, SAM–7791 (Fig. 85A), by lectotype designation herein, together with SAM–PDB570, 4305a, b and PRV–21, all preserved as internal moulds.

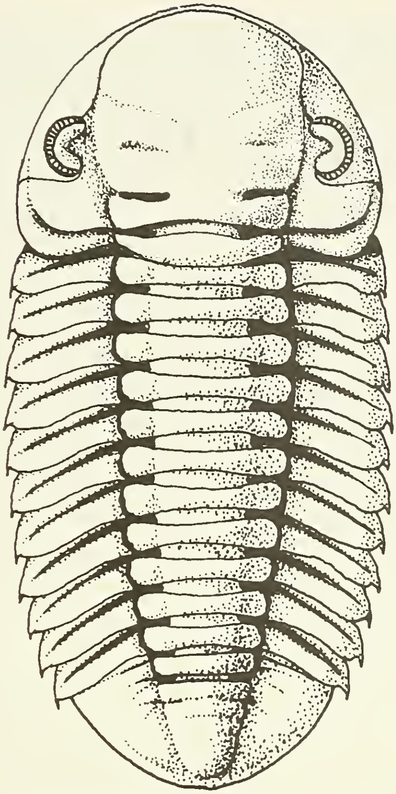

Fig. 84. *Phacopina convexa* Eldredge & Braniša. A reconstruction based upon the figured material. × 3.

Description

Cephalon. The cephalon is semi-elliptical in outline, weakly convex, and with a length/width ratio of about 0,50. The axial furrows are moderately impressed, straight, and diverge slightly to the anterior. The frontal lobe is elliptical to subrhomboidal, with no discernible auxiliary impression system. The glabella is distinctly wider (trans.) than long (sag.), with a length/width ratio of 0,84. One of the most distinctive features of this species are the 3p furrows which are distally strongly impressed and connected to the axial furrows. Adaxially, however, they are very fine and weakly impressed, and barely discernible. This gives the impression of very short 3p furrows. The 2p furrows are lightly impressed, anteriorly convex to almost straight, and do not connect with the axial furrows, with the result that L2 and L3 coalesce distally. The 1p furrows are very deep, anteriorly concave, and strongly connected to the axial furrows. The L1 lobes are rather narrow (exsag.), broadening slightly

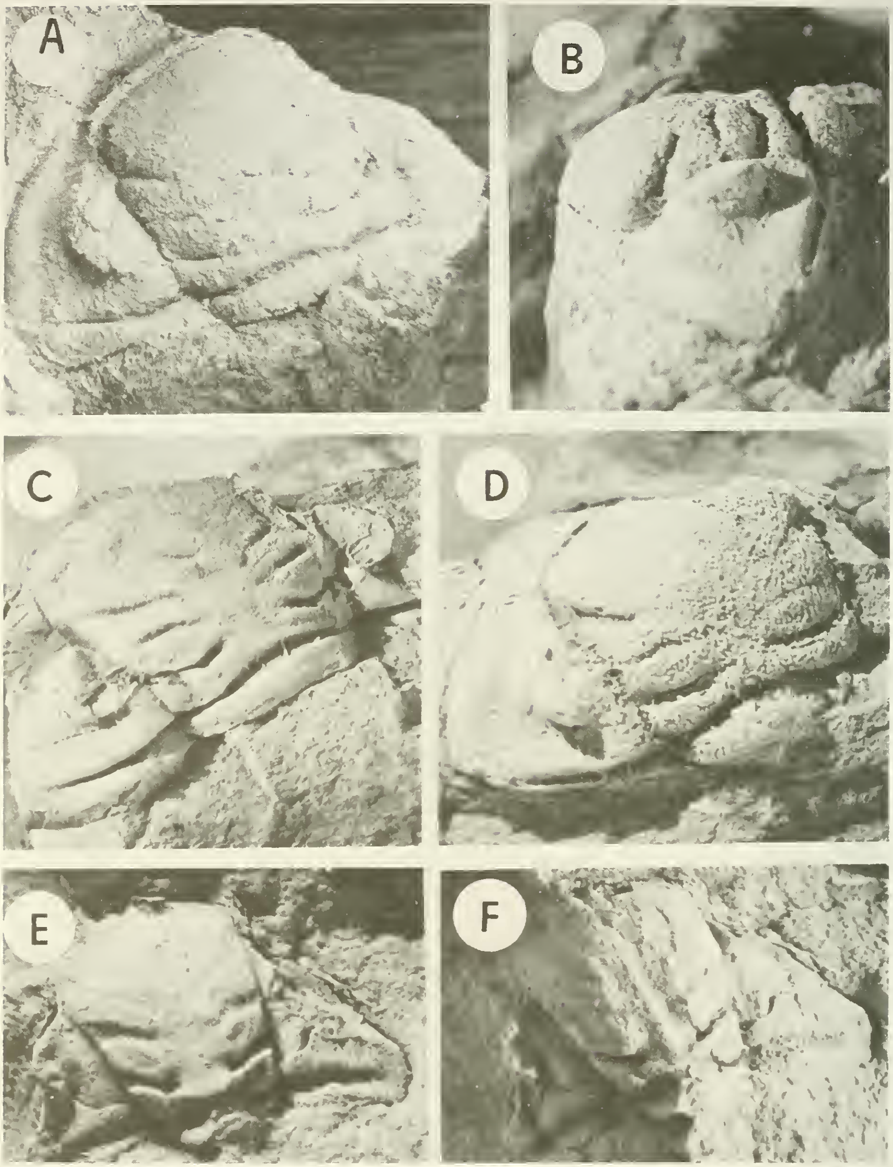

Fig. 85. A–B, D. *Phacopina lakei* (Reed). A. SAM–7791, the lectotype and original of Reed (1925*a*, pl. 9 (fig. 4)). × 2,3. B, D. PRV–21. Note the short 3p furrows, distinct anterior border, large eyes, convex anteriorly 2p furrows and long (trans.), narrow L1 lobes. × 2,6. C. *Oosthuizenella ocellus* (Lake). PRV–37. × 2,6. E–F. *Phacopina?* sp. nov? PRV–119. Note the deeply impressed 2p furrows, sagittal ridge to the median area and truncate frontal lobe. × 2,6. All preserved as internal moulds.

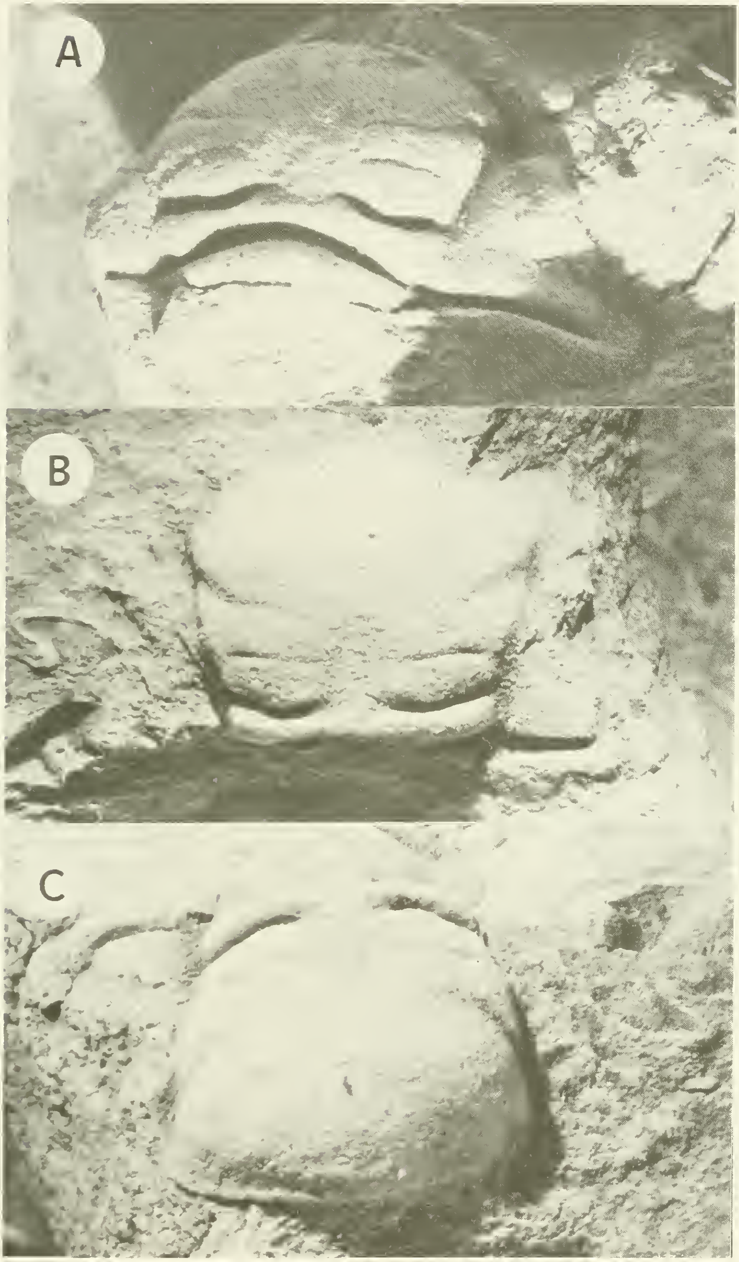

Fig. 86. *Phacopina lakei* (Reed). A. SAM–PDB4305a. B–C. SAM–PDB4305b. Both preserved as internal moulds and both × 2,6.

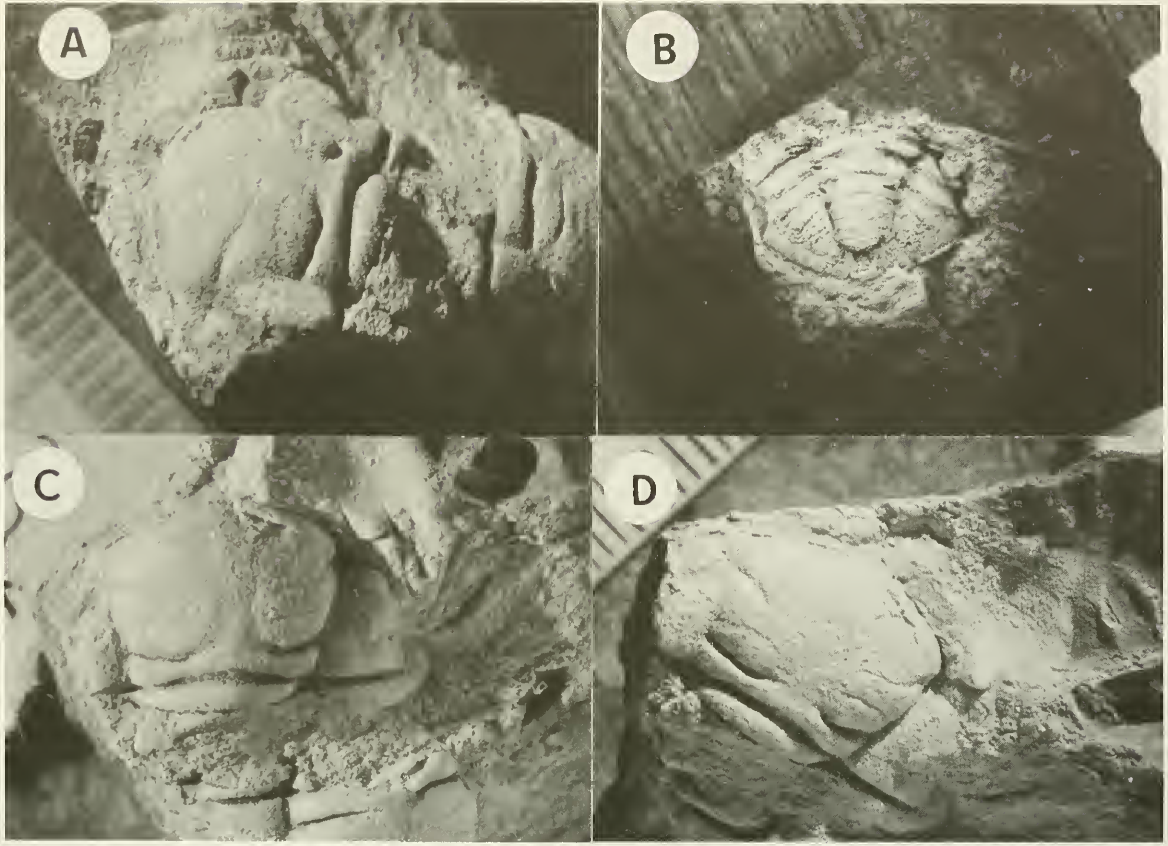

Fig. 87. A, C–D. *Phacopina lakei* (Reed). SAM–PDB4305a. Note the faint sagittal ridge to the median area, weakly impressed, anteriorly convex 2p furrows, and breadth of the glabella. ×2. B. Cf. *Bainella gamkaensis* Rennie. SAM–7794, the lectotype of *Phacops (Bouleia?) sharpei* Reed (1925*a*, pl. 9 (fig. 6)). ×1,5. All specimens preserved as internal moulds.

Fig. 88. *Phacopina lakei* (Reed). SAM–PDB570, a crushed example with a mineralized cuticle. The associated pygidium is too poorly preserved for satisfactory identification but may belong here. × 2,5.

abaxially. The occipital furrow is moderately deep, arched forward sagittally, and with deep apodemal pits distally. The occipital ring is smooth and broadest sagittally. The cheeks are moderately convex, weakly down-turned, with deeply impressed posterior border furrows that curve forward distally. The lateral border furrows are shallow and ill-defined. The posterior border is prominent, broadening (exsag.) abaxially, as are the lateral borders. There is a distinct, narrow, anterior border that is visible in dorsal view. The eyes are relatively large, about 40 per cent of the exsagittal length of the cephalon. The writer was unable to discern the small profixigenal spines which were alleged to occur (Reed 1925*a*: 155) just posterior to the intersection of the facial suture with the lateral border. There is no evidence for the anterior branches of the facial sutures cutting the lateral extremities of the frontal lobe, and the posterior branches meet the lateral borders slightly in front of the posterior margins of the eyes.

Discussion

This species is currently known only from cephala and hence may be based upon a different part of the same animal as *Phacopina hexensis* (Reed). Until more material is available, however, it is retained as distinct.

Fig. 89. A. *Bainella arbuteus* (Lake). SAM–7178, the original of Lake (1904, pl. 24 (fig. 4)), preserved as an internal mould. × 2. B. *Pennaia?* sp. juv. indet. Reed's (1925*a*, pl. 9 (fig. 5)) figured syntype of *Phacopina lakei* (Reed). × 4,5.

Phacopina is closely related to *Pennaia* and they seem to be sister taxa, perhaps both derived from the Silurian *Andinacaste*. As such they share many features in common and, in the absence of complete specimens, discrimination is not always easy. The present species is assigned to *Phacopina* because of its very broad (trans.) cephalon and glabella, the latter bluntly rounded anteriorly and with a distinct anterior border. The L1 lobes are narrower (exsag.) and longer (trans.) than is typical of *Pennaia*, and the 2p furrows are much more weakly impressed.

Reed's (1925*a*) small, figured syntype (Fig. 89B) of *Phacopina lakei* emphasizes this problem. Reed considered this example to have an entire pygidium but, as can be seen from Figure 89B, the margins are obscured by matrix. As such it is uncertain whether the border was entire, as in *Phacopina*, or with minute spinules, as in *Pennaia*. The presence of at least 6 axial rings and 5 distinct pairs of pleural ribs to the pygidium tends to suggest that this specimen is a juvenile *Pennaia*. This is supported by the straight 2p furrows and posterior border furrows to the cephalon. As such the writer is inclined to identify this specimen as *Pennaia?* sp. juv. indet.

Occurrence

Phacopina lakei (Reed) is currently known with certainty only from the Voorstehoek Formation of the Bokkeveld sequence.

Phacopina? sp. nov?

Figs 85E–F, 90

Material

A single cephalon, PRV–129, preserved as an internal mould, from the Hottentotskloof, 30 km north-east of Ceres.

Description

Cephalon. The cephalon has been slightly crushed, but was clearly much wider (trans.) than the sagittal length, and moderately convex. The glabella is subtrapezoidal in outline, with straight, rather deep axial furrows diverging

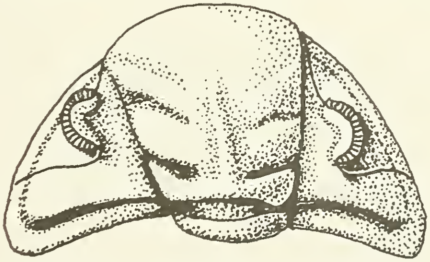

Fig. 90. *Phacopina?* sp. nov?
A reconstruction of the cephalon based upon PRV–119.
×3.

anteriorly and an abruptly truncate, weakly convex anterior margin. It is longer than wide, with a length/width ratio of 1,05, and a distinct sagittal ridge to the median glabellar area. The 3p furrows are very poorly developed, almost obsolete; they are sinuous and directed strongly posteromedially, and weakly connected to the axial furrows. The 2p furrows are moderately impressed, anteriorly convex, and weakly connected to the axial furrows. The 1p furrows are very deep and directed strongly posteromedially, so that the L1 lobes broaden (exsag.) considerably abaxially, and are distinctly connected to the axial furrows. The occipital furrow is broad, anteriorly convex, and with deep apodemal pits distally. The occipital ring is poorly preserved, but seems to have been smooth and of more or less constant width. The cheeks are subtrigonal, weakly convex, and with deep, straight posterior border furrows and subrounded genal angles. The eyes are poorly preserved, but seem to have been about one-third of the exsagittal length, while the facial sutures could not be discerned. The surface of the cephalon is finely granulose.

Discussion

The present example differs from *Phacopina lakei* (Reed) in having a glabella that is longer than wide (trans.), with almost obsolete 3p furrows and moderately impressed 2p furrows that weakly connect with the axial furrows, a sagittal ridge to the median glabellar region, L1 lobes that broaden (exsag.) markedly distally, and straight posterior border furrows to the cheeks.

'*Acastoides*' *koukharskii* Baldis & Longobucco (1977*b*: 171, figs 1–3) bears a superficial resemblance to the above example, but has deeply impressed 3p furrows, and an ellipsoidal to rhomboidal frontal lobe, while lacking a sagittal ridge to the median area.

Phacopina padilla Eldredge & Braniša (1980: 251, fig. 24A–F) has a more rounded cephalon, larger eyes, narrower (exsag.) L1 lobes, weaker 2p furrows that become obsolete distally, and genal spines. *Phacopina convexa* Eldredge & Braniša (1980: 248, figs 2B, 22–23A) also has a more rounded cephalon and weaker 2p furrows that become obsolete distally, with the fusion of the L2 and L3 lobes.

Phacopina braziliensis (Clarke) (Eldredge & Braniša 1980: 240, figs 20A–C) has much larger eyes placed further backward, obsolete 2p and 3p furrows, transverse 1p furrows and narrow (exsag.) L1 lobes, and a more rounded cephalon than the present material.

Phacopina cf. *padilla* Eldredge & Braniša, 1980

Figs 91–92

Compare

Phacopina padilla Eldredge & Braniša, 1980: 251, fig. 24A–F.

Material

A single internal mould, SAM–8965, in black carbonaceous shale and thus from the Gydo Formation.

Description

Only the cephalon is known from South African material. It is semicircular in outline, weakly convex, and with a glabella that expands slightly to the anterior. The axial furrows are fairly deeply impressed, except between the eyes and L3 lobes where they become almost obsolete. There are distinct axial furrow pits. The 3p furrows are rather weakly impressed, almost straight, and directed strongly posteromedially; they appear to connect weakly with the axial furrow pits. The 2p furrows are straight, transverse, and distally obsolete, with

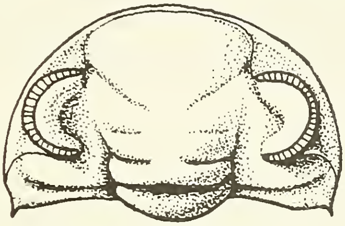

Fig. 91. *Phacopina* cf. *padilla* Eldredge & Braniša. A reconstruction of the cephalon based upon SAM–8965. × 5.

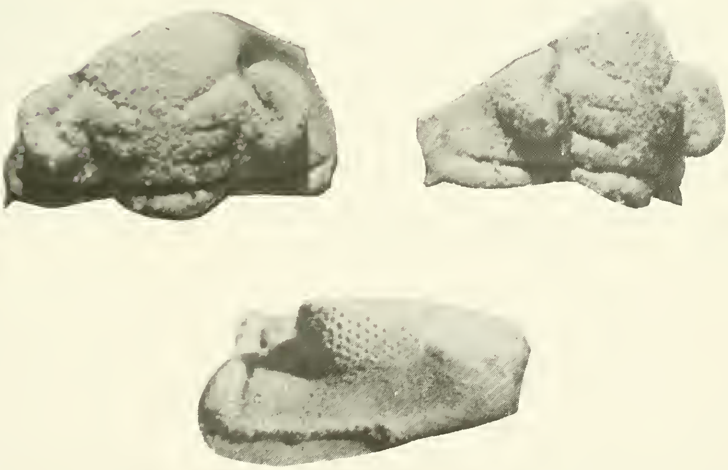

Fig. 92. *Phacopina* cf. *padilla* Eldredge & Braniša. SAM–8965, preserved as an internal mould. Note the spiniform processes to the genal angles, the large eyes, moderately impressed 3p furrows, and the weakening of the axial furrows opposite the L3 lobes. Dorsal views × 5, lateral view of visual surface of eye approx. × 8.

the abaxial fusion of the L2 and L3 lobes. The 1p furrows are very deep, transverse, slightly concave to the anterior, and strongly connected to the axial furrows. The occipital furrow is deep, broadest sagittally, and with apodemal pits distally. The smooth occipital ring is somewhat inflated, and broadest sagittally. The cheeks are rather convex, with deep posterior furrows that are slightly concave to the anterior, and broad, shallow, indistinct lateral furrows. The posterior borders broaden (exsag.) slightly abaxially, and the well-rounded genal angles bear minute spines. The eyes, situated between the 1p and 3p furrows are large, about 50 per cent of the exsagittal length of the cephalon, and strongly arcuate. The palpebral lobes lie in the same horizontal plane as the median area of the glabella. The visual surface of the eye comprises about 25 vertical files, with 6 ocelli in the central file. The anterior ramus of the facial suture may, just, transect the lateral edge of the frontal lobe, while the posterior branch is initially directed anterolaterally, before recurving strongly to meet the lateral margin just in front of the genal spinules.

Discussion

The very small size, large eyes, and minute genal spines suggest comparison of the Bokkeveld example with *Phacopina padilla* Eldredge & Braniša. It differs from the Bolivian material mainly in having more deeply impressed 2p and 3p furrows, and distinct axial pits opposite the distal terminations of the 3p furrows. The differences are slight and probably due to intraspecific variation and differences in preservation.

Phacopina correlator (Clarke) (Eldredge & Braniša 1980, fig. 20F–G) from the Oriskany of Becraft Mountain is also very close to the present species. It seems to differ mainly in the greater expansion of its frontal lobe, with slightly smaller eyes, and subacuminate genal angles that apparently lack spinules.

Occurrence

Phacopina padilla Eldredge & Braniša is currently known from the lower part of the Icla Formation at Padilla, Bolivia, and perhaps from the Gydo Formation of the Bokkeveld sequence.

Genus ***Renniella*** gen. nov.

Type species ***Renniella rossouwi*** gen. et sp. nov.
by original designation herein

Diagnosis

A calmoniid with a strongly inflated, protuberant, frontal lobe showing a typical calmoniid auxiliary impression system. There is a pronounced posterior median impression that is connected to the proximal ends of the 3p glabellar furrows and serves to isolate the frontal lobe. The glabellar axial furrows are moderately deep, diverging strongly to the anterior, and with deep axial furrow pits at the distal terminations of the 3p furrows. The latter are strongly impressed, but weaken distally and connect only very faintly with the axial furrows. The 2p furrows are transverse, deepest medially and becoming effaced distally. The 1p furrows are deep, short, parallel to the 2p furrows, and distinctly connected to the axial furrows. Proximally, the 1p furrows show a weak bifurcation. There is a small but distinct tubercle (spine base?) between the medial bifurcations of the 1p furrows. The L3 lobes broaden (exsag.) distally where they coalesce with the L2 lobes which are of constant width. The L1 lobes are relatively broad (exsag.) and also of constant width. The occipital furrow is transverse with deep apodemal pits distally. The eyes seem to have been raised on palpebral prominences and appear to be small, only about one-quarter of the exsagittal length of the cephalon. The characters of the genae and facial sutures are unknown. Certainly, the anterior branch of the facial suture does not transect the lateral corners of the frontal lobe. The anterior border is very narrow and overhung by the frontal lobe.

Etymology

The generic name *Renniella* is for Professor J. V. L. Rennie, vice-chancellor of Rhodes University, Grahamstown, who contributed greatly to an understanding of the Bokkeveld trilobites. The specific name is for Mr P. J. Rossouw of the Geological Survey, Pretoria, who has added much to our knowledge of the Bokkeveld succession.

Discussion

Renniella is very close to *Tarijactinoides*, as redescribed and rediagnosed by Eldredge & Braniša (1980), but differs from that genus in lacking a prominent spine to the frontal lobe; instead it has a median tubercle (spine?) between the adaxial bifurcations of the 1p furrows. In addition, the glabellar furrows of *Renniella* are not connected medially, its 3p furrows do reach the axial furrows, it possesses prominent axial furrow pits, the occipital furrow is

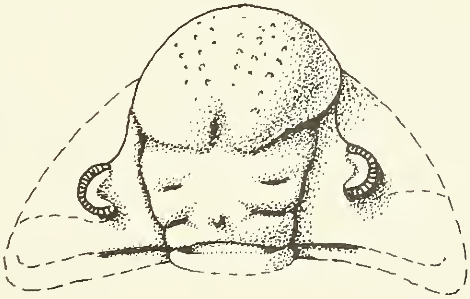

Fig. 93. *Renniella rossouwi* gen. et sp. nov.
A reconstruction of the cephalon based upon PRV–1015.
×3.

Fig. 94. *Renniella rossouwi* gen. et sp. nov. PRV–1015, an internal mould. Note the isolated frontal lobe, deep axial furrow pits, distinct tubercle between the adaxial terminations of the 1p furrows, and the weak adaxial bifurcation of the latter. × 3.

transverse, and the L1 lobes are relatively broader (exsag.) than in *Tarijactinoides*. So far as can be judged, however, the two genera are closely related.

Renniella also bears a superficial resemblance to *Bainella gamkaensis* Rennie. It differs from that species in having smaller eyes that are closer to the axial furrows, 3p furrows joined medially to isolate the frontal lobe, 2p furrows that are deepest medially and effaced distally, 1p furrows that show a weak adaxial bifurcation, broader (exsag.) L1 lobes, L2 and L3 lobes that coalesce distally, and a distinct median tubercle between the adaxial bifurcations of the 1p furrows.

Renniella rossouwi gen. et sp. nov.

Figs 93–94

Material

A single cranidium, PRV–1015, preserved as an internal mould.

Holotype

The above specimen, PRV–1015, by monotypy; it is from the main tunnel at Hex River.

Description

As for diagnosis.

Discussion

The above specimen, although fragmentary, is so distinctive that the writer has little hesitation in creating a new genus and species to accommodate it.

Occurrence

Renniella rossouwi gen. et sp. nov. is currently known only from the Bokkeveld Group. Its state of preservation suggests the Gydo Formation.

Genus *Bainella* Rennie, 1930

Type species *Bainella bokkeveldensis* Rennie, 1930;
by original designation

Discussion

There are unfortunately still nomenclatural problems concerning the generic names *Anchiopella* and *Bainella* (cf. Lespérance & Bourque 1971: 202) and it is proposed to approach the ICZN (Cooper 1982) to have the former name formally suppressed in favour of *Bainella*.

Eldredge & Braniša (1980) have recently provided an emended diagnosis and detailed discussion of *Bainella* to which little can be added. It should be noted, however, that not all species (e.g. *B. africana* and *B. gamkaensis*) possess a terminal spine to the pygidium, while *B. arbuteus* (Lake) possesses variably developed fulcral spines. Moreover, the genal spines of *B. africana* (Salter) are situated slightly inside (adaxial) of the genal angles in maturity and are curved sagittally at their tips. Also, the writer does not personally favour the use of the term 'lappets' for the minute spinules that ornament the pygidial margins of *B. insolita* and *B. arbuteus* and do nothing more than provide the margin with a scalloped appearance. These are clearly equivalent to the 'interior denticles' of Harrington *et al.* (1959).

Eldredge & Braniša (1980: 202–203) created the new subgenus *Belenops* for *Acastoides insolitus* Wolfart and *Bainella gamkaensis* Rennie, diagnosed as '. . . species of *Bainella* with anterior cephalic margin distinctly rounded, and anterior glabellar lobe greatly inflated. Anterior branch of facial suture transecting a relatively small portion of the anterolateral corner of anterior glabellar lobe. Glabellar furrows 3p sinuous; 1p glabellar furrows wholly confluent with axial furrows. Anterolateral region of cephalic doublure sharply recurved dorsally, confluent with dorsal cephalic surface. Occipital spine generally present, occasionally absent in some populations. Thorax and pygidium as for genus.' While there are obvious similarities when cephalic synapomorphies are considered, the picture changes somewhat when the pygidial characters of the various *Bainella* species are compared. As currently defined, the subgenus *Belenops* is of questionable value and it is not used here.

Bainella africana (Salter, 1856)

Figs 33B, 39A–B, 50F, 57A, 58A–D, 66B, 67B, 68A, 70, 76E, 77E, 78A, 95–96, 97B–F, 98B, D, 99A–B, 100.

Phacops (Cryphaeus) africanus Salter, 1856: 218, pl. 25 (figs 1, 3, 5, 8 only).
Phacops africanus Salter, Lake, 1904: 205, pl. 24 (figs 6–8).
Phacops crista-galli (Woodward) Lake, 1904: 205, pl. 24 (fig. 5)).

Phacops acacia Schwarz, 1906: 398, pl. 10 (fig. 4).
?*Dalmanites (Mesembria) acacia* (Schwarz) Clarke, 1913: 116, pl. 5 (figs 5–9).
Phacopidella africana (Salter) Williams & Breger, 1916: 287.
Dalmanites (Anchiopella) africanus (Salter) Reed, 1925*a*: 122, pl. 8 (fig. 1).
?*Dalmanites (Anchiopella) baini* Reed, 1925*a*: 129, pl. 9 (figs 1–3).
Phacops (Phacopina) hiemalis Reed, 1925*a*: 159, pl. 10 (fig. 8 only).
Bainella? africanus (Salter) Rennie, 1930: 345.
Bainella acacia (Schwarz) Rennie, 1930: 348, pl. 10 (fig. 5), fig. 1.
?*Bainella baini* (Reed) Rennie, 1930: 345.
Bainella bokkeveldensis Rennie, 1930: 349, pl. 10 (figs 1–4). Struve (*in* Harrington *et al.*), 1959: 0484, fig. 383,2. Eldredge & Ormiston, 1979: 158. Eldredge & Braniša, 1980: 199, fig. 3.
?*Bainella (Bainella)* '*acacia*' (Clarke) (*non* Schwarz) Eldredge & Braniša, 1980: 201, figs 2J, 4–5.

Material

The holotype, by lectotype designation herein, BM–In28608 (Fig. 96), together with BM–9857, BM–In23972, 24100, 24102, 28601, 28603, 28605, 28609–28611, 28615, 29235, PRV–57, 92, 292, BPI–i239, SAM–782, 7179, 7182, 9606, SAM–PDB461, 3076, 3080, 3945, 4222, SMC–A2961, 2962, AM–32, 2124, SU–K434, 461, and RO–22, 30, 48, 193, 221, 223, 708, 710, 749, 756, 764, 779, 784, C75–C76, E14–E36, E53, E75, L18–L19, L59, L74, and P20.

Description

Cephalon. The cephalon is moderately convex, subtrigonal to subpentagonal in dorsal outline, and much wider than the sagittal length. The surface is finely granulose but lacks coarse tuberculation and for all intents and purposes may be regarded as 'smooth'. The glabella is slightly convex, distinctly pentagonal in outline, and with variable segmentation. The 3p and 2p glabellar furrows are generally very weak and indistinct; the 3p furrows are directed anterolaterally, curving forward distally so that they are not confluent with the axial furrows; the 2p furrows are transverse, perhaps slightly convex to the anterior and do not reach the axial furrows so that the L2 and L3 lobes coalesce distally. The 1p furrows are transverse, with deep adaxial, linear apodemal pits but only weakly connected to the axial furrows. The latter are broad, shallow, pronounced, almost straight and diverge slightly to the anterior. The occipital furrow is broadest sagittally with deep linear apodemal pits abaxially behind the L1 lobes. The posterior border furrows are moderately deep and broad, but shallow abaxially, and the lateral border furrows are wide, very shallow and indistinct. There is a very narrow anterior border, with a weak median frontal process (cf. BPI–i239), separated from the glabella by a very narrow but distinct preglabellar furrow. The occipital ring is of constant width and bears a long median spine, and the posterior borders broaden abaxially. The genal angles are obtusely angulated to subrounded, behind which are prominent, posteriorly directed spines that are curved adaxially at their distal terminations. Since these hook-like spines are not a direct continuation of the lateral margins of the cephalon, they are perhaps best described as metafixigenal spines. However, in juveniles (Fig. 97D) they are true genal spines and, as such, their

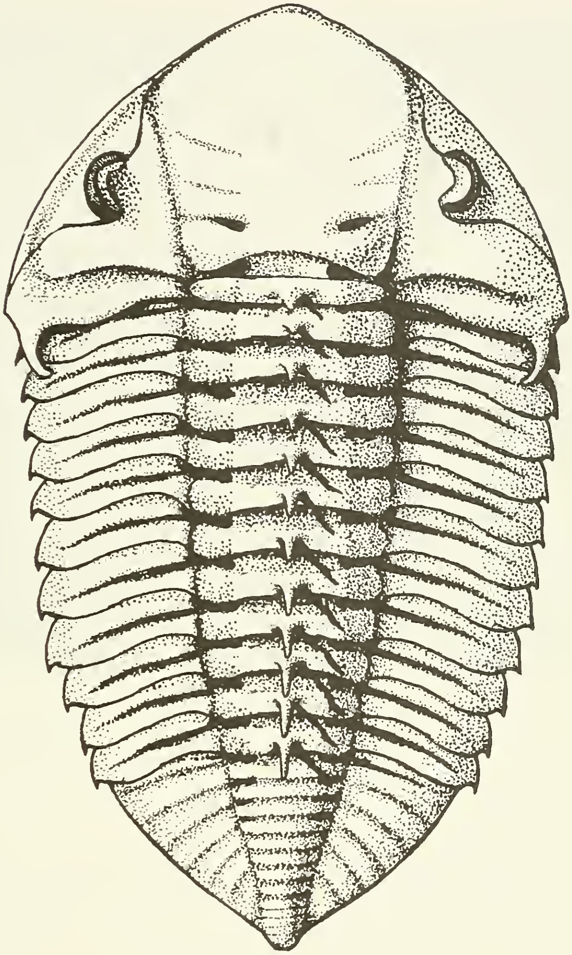

Fig. 95. *Bainella africana* (Salter).
A reconstruction based upon the available material.
× 1,5.

position changes somewhat during ontogeny. The cheeks are moderately convex, subtrigonal in outline, with the eyes raised on well-developed palpebral prominences. The eyes are smallish, about one-third of the exsagittal length, and comprise vertical files of lenses, with 7 ocelli in the central file. There are distinct anterior ocular ridges that follow the line of the anterior facial sutures to which they lie immediately adaxial, and are confluent with the anterior border. The hypostoma is wider than its sagittal length with sharply pointed anterior wings reflexed vertically. The central body is almost circular, weakly convex and separated from the posterior and lateral borders by a distinct groove. The tiny maculae are situated laterally, just posterior to the proximal

Fig. 96. *Bainella africana* (Salter). BM–In28608, the lectotype and original of Salter (1856, pl. 25 (fig. 8)), preserved as an internal mould. × 4.

margins of the anterior wings. Border spines are absent from the posterolateral margins of the hypostoma on the internal mould.

Thorax. The thorax has a rather broad axis, about one-third of the thoracic width, which tapers slightly to the posterior. The axial rings are very rounded, constricted sagittally and with long median spines. They broaden distally and are separated by well-developed ring furrows, the latter with distinct apodemal pits abaxially. The pleurae are moderately convex, with a fairly distinct fulcrum; they are divided into prominent anterior and posterior moieties by deep pleural grooves and are separated by distinct interpleural furrows. Distally the pleurae bear short, blunt posteriorly directed spines.

Pygidium. The pygidium is moderately convex and subtrigonal in outline, with a prominent axis tapering posteriorly and terminating in a bluntly rounded tip. The axis comprises 8–10 rings, about as wide as the ring furrows, and there is no post-axial field. The first 2–3 ring furrows bear apodemal pits distally, and the last few rings are indistinct. There are no median tubercles or spines to the axial rings. The pleural fields are triangular, rather convex, and comprise 5 pairs of pleurae, of which the posterior pair are reduced and insignificant. The pleurae have deep, broad pleural grooves, and the interpleural furrows are narrow and indistinct. The pleural grooves do not reach the pygidial margin, so that there is a narrow, smooth border. Because the lateral margins of the pygidium are anteriorly convex and posteriorly concave, this creates the impression that the axis extends well beyond the posterior margin in some individuals (Fig. 76E).

Discussion

Regarding *Phacops africanus*, Reed (1925*a*: 122) commented that '. . . the primary difficulty in determining the true characters of *Ph. africanus* of Salter lies in the uncertain identification of the first specimen figured by Salter under this name . . . it may be regarded as fairly certain that the poor specimen in the British Museum, numbered 11295, from Leo Hoek, was the one from which Salter's partially restored figure was drawn'. Reed (1925*a*), however, did not select a lectotype but regarded *Ph. africanus* as a recognizable species on the basis of supplementary topotype material. Rennie (1930: 346) gave a comprehensive discussion of Salter's species and suggested that Lake (1904: 206) had selected Salter's (1856, pl. 25 (fig. 1)) first figure '. . . as the type figure of the species, but was unable to recognize in the collections the specimen from which the figure was taken'. He also refuted Reed's (1925*a*) suggestion that BM–11295 was the original of Salter's figure 1. Hence Rennie (1930: 347) was led to conclude that since '. . . the type has disappeared and the original description of the species (having been based on several unrelated individuals) is misleading, *Ph. africanus* should be considered a *nomen dubium*, the name to be retained for Salter's first figure only'.

Contrary to Rennie's (1930) suggestion, however, Lake (1904) *did not* select a lectotype for *Phacops africanus*; his exact words were '. . . Salter's *Phacops africanus* appears to include at least four distinct species, and unfortunately the original of his fig. 1 has not yet been recognized with certainty. It seems, however, to be identical with the specimens here described, and accordingly I have adopted his name for this form' (p. 206). Such a statement cannot be construed as a lectotype designation, and hence *Phacops africanus* is still without a holotype. Since the original of Salter's plate 25 figure 1 cannot be recognized, either because the figure is composite or the original specimen has been lost, it is proposed to select as holotype, by formal lectotype designation herein, the original of Salter's plate 25, figure 8, BM–In28608, which formed part of Salter's syntype series and is here refigured (Fig. 96).

With the selection of a recognizable lectotype, together with the abundant topotype material now available, it is clear that *Bainella acacia* (Schwarz) (Fig. 66B) and *B. bokkeveldensis* Rennie must become junior subjective synonyms of *B. africana* (Salter). In addition, the writer has had the opportunity to study the holotype cephalon, by monotypy, of *Phacops (Phacopina) hiemalis* Reed (1925*a*: 159, pl. 10 (fig. 8 only)), BM–In24100. The occipital ring is damaged (due to the breaking off of the median spine?) and the genal spines seem to have been broken off. In all other characters this specimen agrees with *B. africana*, of which it is herein considered a junior subjective synonym.

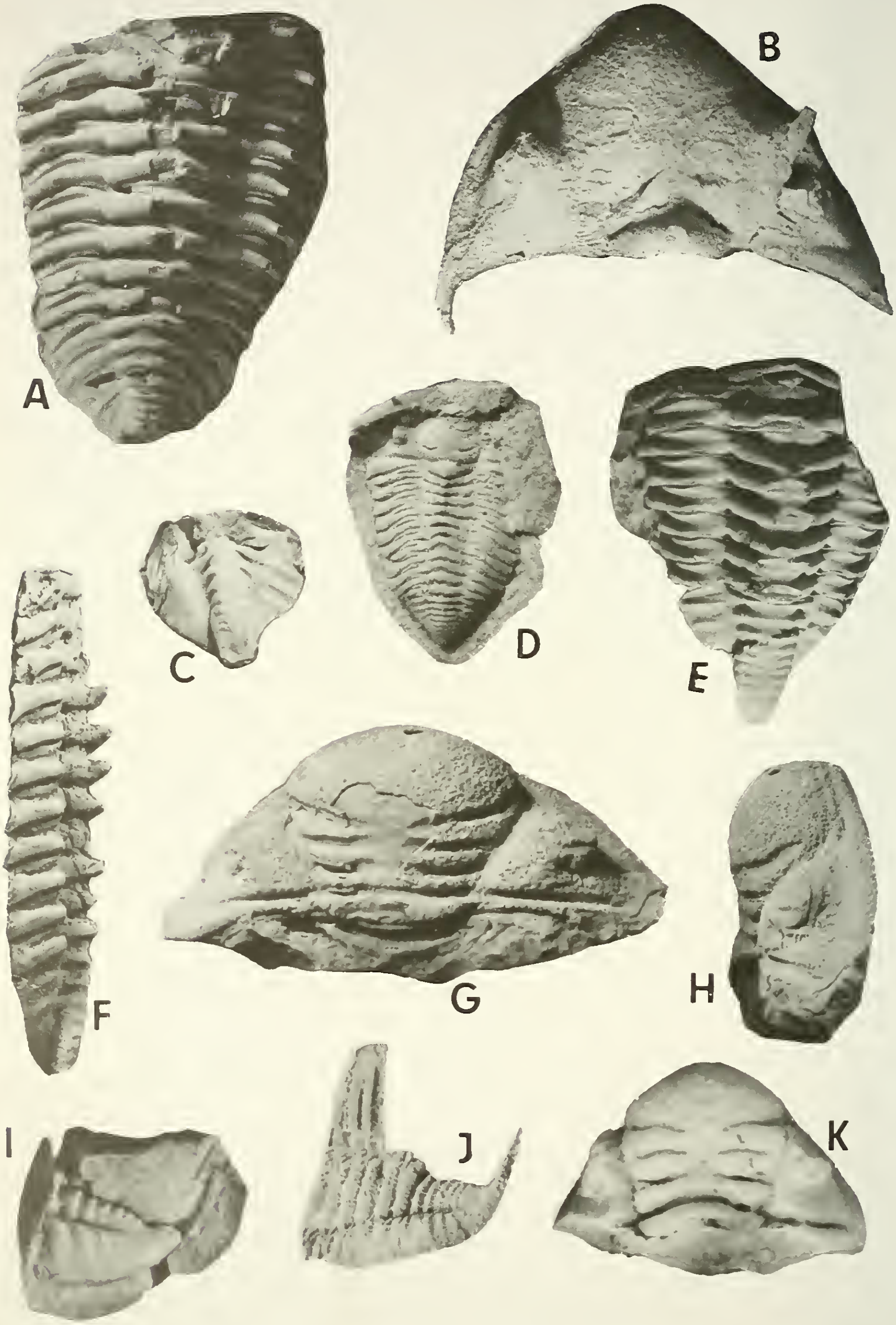

Fig. 97. A. *Bainella arbuteus* (Lake). Latex cast of an external mould, RO–23. Note the spine bases to the fulcral axes of the thorax. B–F. *Bainella africana* (Salter). B. RO–749, an internal mould. C. SAM–7182, the original of Lake (1904, pl. 24 (fig. 8)), preserved as an internal mould. D. Latex cast of an external mould, RO–221. Note the shape and position of the genal spines. E. RO–710, preserved as an internal mould. F. An unnumbered specimen in the South African Museum, preserved as an internal mould. G–H. *Bainella gamkaensis* Rennie. RO–750, a cephalon retaining cuticle. I–J. *Bainella cristagalli* (Woodward). I. RO–790, an internal mould. J. RO–66, a crushed example retaining cuticle. K. *Phacopina?* sp. RO specimen, preserved as an internal mould. All × 1.

Bainella baini (Reed) (1925*a*: 129, pl. 9 (figs 1–3)) was based upon several specimens preserved as dorsoventrally flattened internal moulds in greyish, micaceous sandstone. Since Reed (1925*a*) had a number of specimens available to him, it is clear that lectotype designation is required. Consequently, the original of his plate 9, figure 1, SMC–A2961 (Fig. 100B herein), is herein selected as lectotype. Reed (1925*a*: 131) distinguished *B. baini* from *B. africana* in that '. . . the glabella is more pentagonal, the two pairs of anterior furrows are stronger and deeper, the eyes are larger, and the ornamentation is much coarser . . . the thoracic segments of *D. baini* seem to have shorter, smaller axial spines'. The glabella of the lectotype, however, is no more pentagonal than many of the topotypes of *B. africana* now available, nor do the eyes seem to have been any larger. Moreover, since the length of the axial spines in *B. africana* is clearly a function of age, this feature cannot be used to distinguish *B. baini*. Indeed, so far as the writer is able to judge, *B. baini* differs from *B. africana* only in possessing relatively deeper 2p and 3p glabellar furrows. Since all material undoubtedly referred to *B. africana* represents nodule preservation, whereas the material referred to *B. baini* is preserved as crushed sandstone internal moulds, it seems that the differences may be artefacts of preservation. In any case, Eldredge & Branišа (1980) have noted considerable difference in the degree of impression of the 2p and 3p glabellar furrows of *Andinacaste chojnacotensis* (Schwarz), and hence the differences between *B. baini* and *B. africana* are of questionable taxonomic importance. There is also another possibility; the lectotype does not preserve genal angles and it is also questionable whether a median spine was present on the occipital ring. The same is also true of a paralectotype, SAM–7786 (Fig. 65B), which also shows weak tuberculation of the frontal lobe more reminiscent of *Kozlowskiaspis ceres* (Schwarz). Another paralectotype cephalon of *B. baini* (Fig. 100A) is extremely poorly preserved; the presence of a median occipital spine cannot be verified, and there appears to be a short, straight genal spine that does not curve inward distally as in *B. africana*. In the writer's opinion *Dalmanites (Anchiopella) baini* Reed is generically indeterminate; it may be based upon either or both of *Bainella* and *Kozlowskiaspis*, while the lectotype is probably a synonym of *B. africana*. It is certainly a *nomen dubium*.

Both Reed (1925*a*) and Rennie (1930) felt that the *Dalmanites (Mesembria) acacia* (Schwarz) figured by Clarke (1913: 116, pl. 5 (figs 5–9)) did not precisely agree with their concepts of *B. acacia*. Eldredge & Branišа (1980: 201, fig. 4) have recently figured a well-preserved cephalon of Clarke's taxon. So far as the writer is able to judge, it differs from *B. africana* only in having slightly deeper 2p and 3p furrows (on the cuticular surface) and longer genal spines that, contrary to the reconstruction of Eldredge & Branišа (1980), were probably curved inward distally. The differences are slight and doubtfully of specific importance but, since this material is in the course of revision by N. Eldredge, its true taxonomic position will soon be apparent.

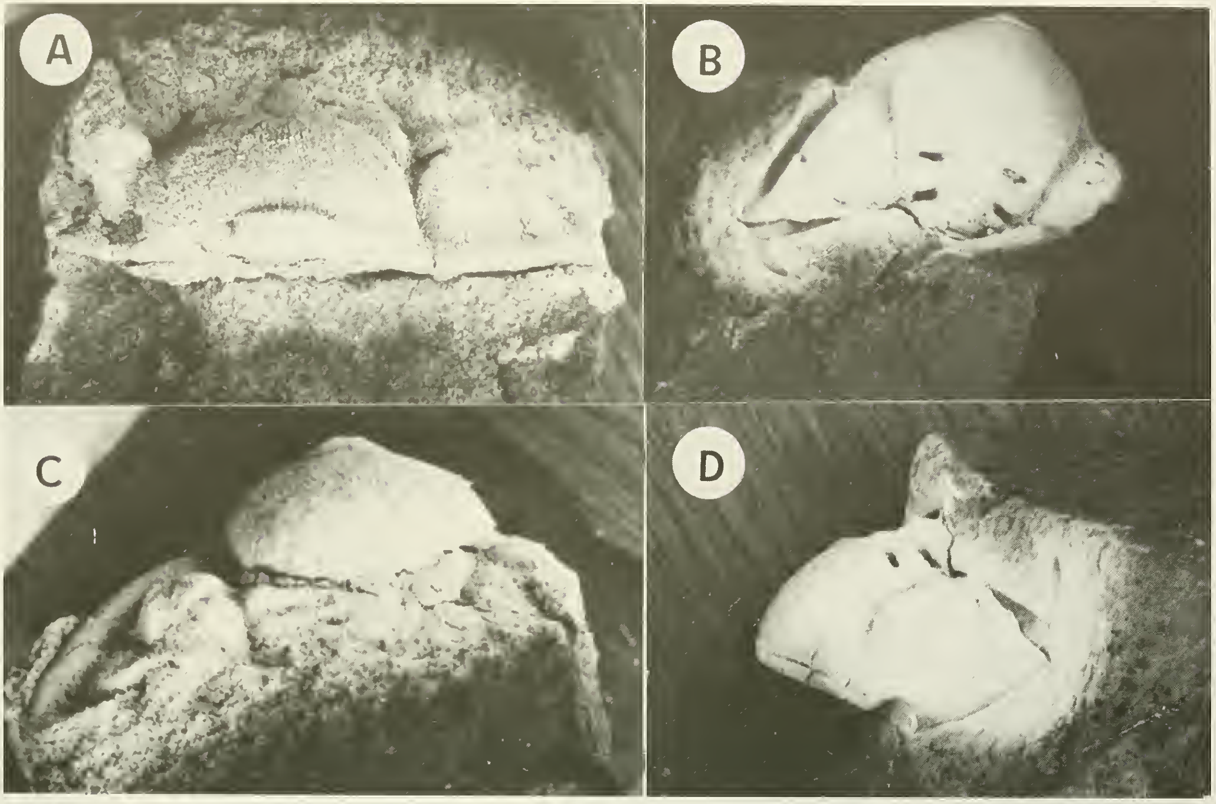

Fig. 98. A, C. *Metacryphaeus caffer* (Salter). SAM–7789, figured by Reed (1925*a*, pl. 9 (fig. 11)). B, D. *Bainella africana* (Salter). SAM–PDB4222, a specimen retaining impressions of the genal spines. Both preserved as internal moulds and both × 1,3.

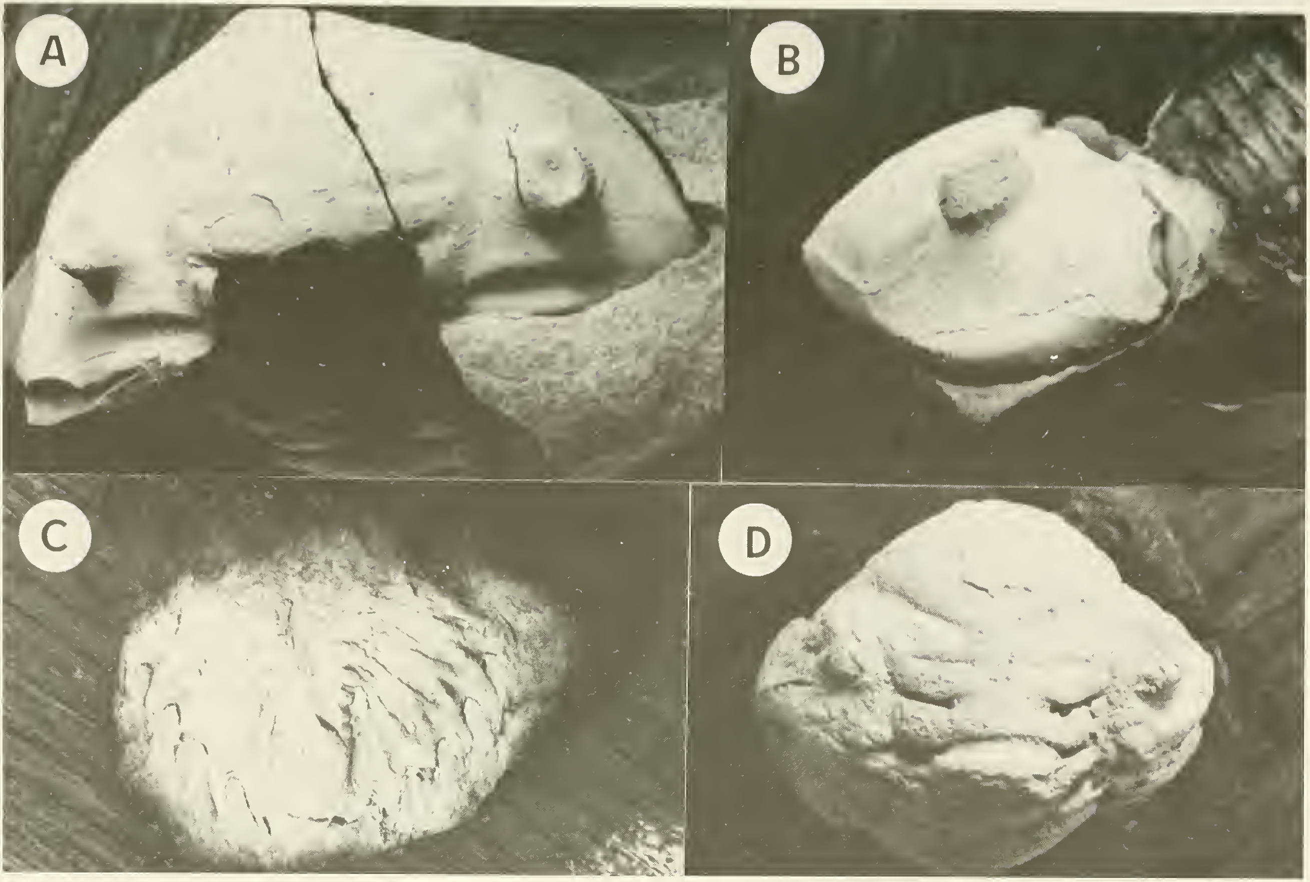

Fig. 99. A–B. *Bainella africana* (Salter). SAM–7179, the original of Lake (1904, pl. 24 (fig. 7)). × 2. C. *Metacryphaeus caffer* (Salter). A specimen in the South African Museum with very prominent lappets. × 1,5. D. *Pennaia* cf. *pupillus* (Lake). An unnumbered specimen in the South African Museum. Note the broad frontal lobe and curved posterior borders. × 1,7. All preserved as internal moulds.

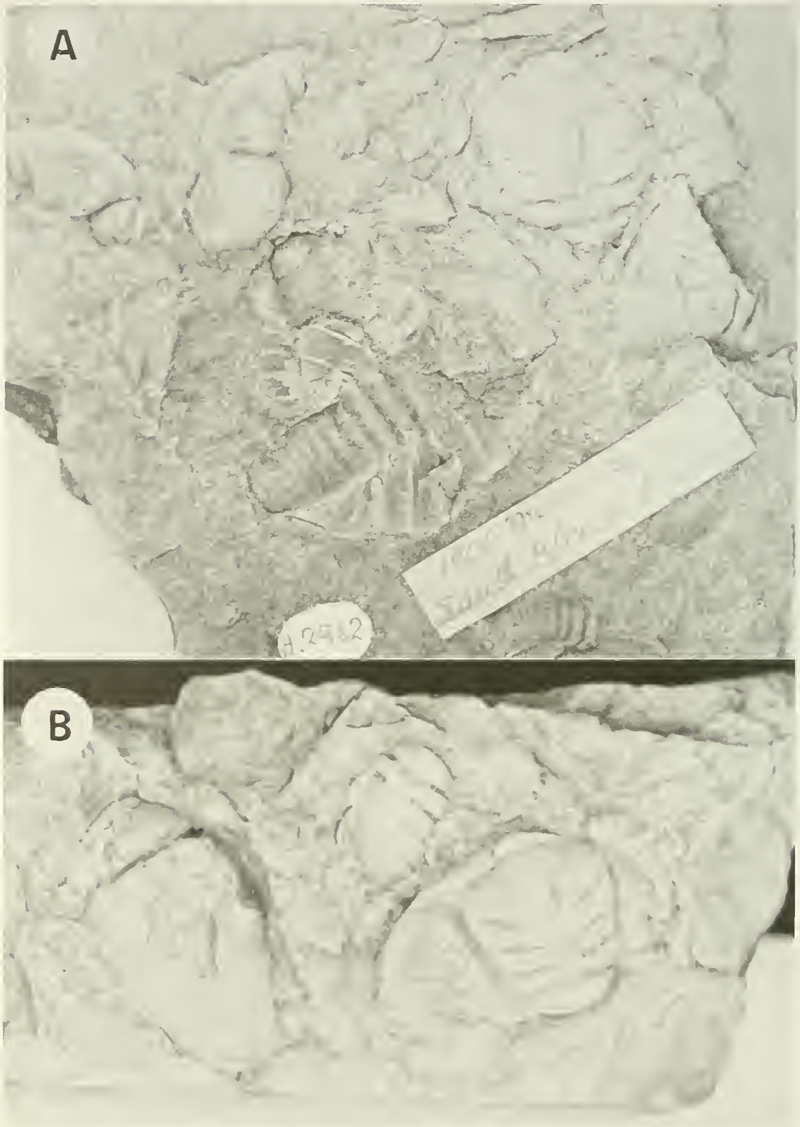

Fig. 100. *Bainella* cf. *africana* (Salter). A. SMC–A2962, syntypes of *Dalmanites (Anchiopella) baini* Reed. B. SMC–A2961, a syntype, herein selected as lectotype, and the original of Reed (1925*a*, pl. 9 (fig. 1)). All preserved as internal moulds and all × 1.4.

Bainella sanjuanina Baldis (1967: 791, pl. 1 (figs 1–4)) is known only from cephala that differ from *B. africana* in having much more deeply impressed 2p and 3p glabellar furrows, the 3p furrows are distinctly sinuous, and internal moulds of the frontal lobe show distinct pitting not seen in *B. africana*. In addition, the L2 and L3 lobes of *B. sanjuanina* are more inflated than those of *B. africana*. The South American species seems to show a curious admixture of *Bainella* and '*Belenops*' characters; it is certainly specifically distinct from *B. africana* and the Malvirn *B.* '*acacia*'.

Bainella africana lacks the coarse tuberculation of *B. arbuteus* and *B. cristagalli*, and is readily separable from *B. insolita* (Wolfart) and *B. gamkaensis* on features of the cephalon and pygidium.

Occurrence

Bainella africana (Salter) is currently known with certainty only from the Gydo Formation of the Bokkeveld sequence, but it may also be present in the Fox Bay Beds of the Falkland Islands.

Bainella arbuteus (Lake, 1904)

Figs 5A–B, 44B, 89A, 97A, 101–103, 104A–E, 105B–C

Phacops arbuteus Lake, 1904: 203, pl. 24 (fig. 2 only).
Dalmanites (Anchiopella) arbuteus (Lake) Reed, 1925*a*: 128.
?*Phacops (Phacopina) hiemalis* Reed, 1925*a*: 159, pl. 9 (fig. 12 only).
Dalmanites arbuteus (Lake) Rennie, 1930: 345.
Non Phacops cf. *arbuteus* Lake, 1906: 428, pl. 40 (fig. 8).

Material

The holotype, by lectotype designation herein, SAM–7181, the original of Lake's (1904) plate 24, figure 2, together with SAM–7178 and perhaps also SAM–7793, as well as RO23–24, 298, 707, 785, 805, C72, and BPI–i240.

Description

Cephalon. The cephalon is moderately convex, with a semicircular dorsal outline, and about twice as wide as the sagittal length. The glabella is pentagonal in outline, moderately convex, with broad, shallow axial furrows that diverge towards the anterior. The entire glabella is coarsely tuberculate, the tubercles varying considerably in size, but there are characteristically 4 large tubercles, in buttonhole fashion, between the adaxial terminations of the 3p glabellar furrows. There is also frequently an enlarged pair of tubercles between, or close to, the adaxial terminations of the 1p furrows, although these are somewhat more variably developed. The 3p glabellar furrows are rather deep, distinctly sinuous, and directed posteromedially at about 70° to the axial furrows with which they are not connected. The 2p furrows are moderately deep, anteriorly convex, and directed slightly posteromedially; they do not connect to the axial furrows. The 1p furrows are subparallel to the 2p furrows, straight, with deep linear apodemal pits adaxially, and distinctly confluent with

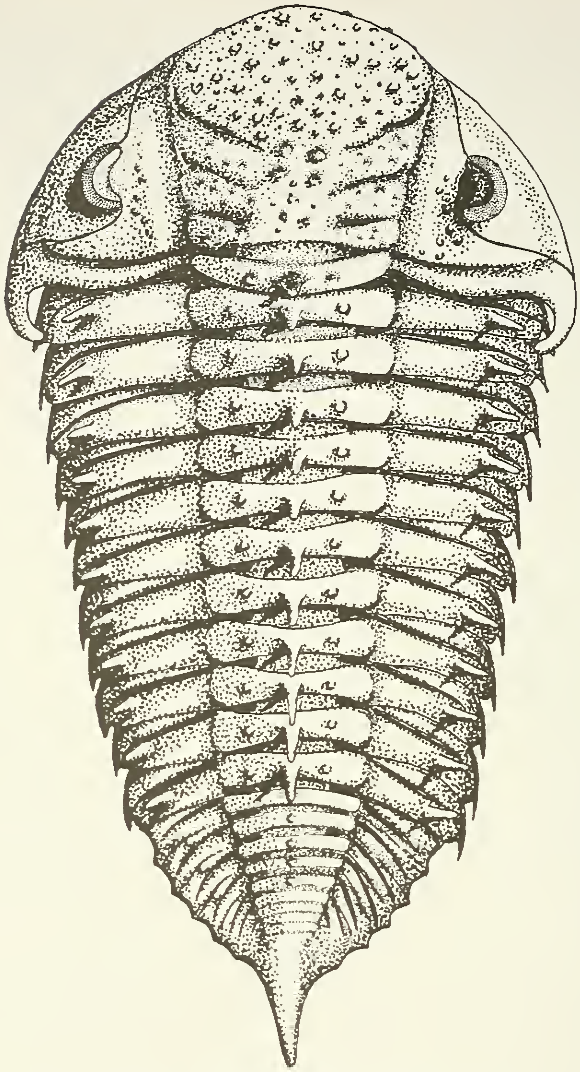

Fig. 101. *Bainella arbuteus* (Lake).
A reconstruction based upon the available material.
× 1.

the axial furrows. The occipital furrow is anteriorly convex, broadest sagittally, and with deep apodemal pits distally. The occipital ring is of uniform width and bears a prominent median spine, flanked on either side by a small tubercle. The posterior border furrows are rather deep and well developed, whereas the lateral border furrows are shallow and ill-defined. The posterior borders broaden (exsag.) abaxially towards the genal angles that are produced into subcylindrical genal spines directed diagonally outwards. The cheeks are subtrigonal, moderately convex, with palpebral prominences on which are situated the eyes. The latter are about one-quarter of the exsagittal length of the cephalon, with their posterior margins opposite the abaxial terminations of the 1p furrows. The librigenae lack tubercles but there are small, scattered tubercles on the fixigenae, running from the posterior border furrow forward to between the eyes and the glabellar axial furrows. The anterior facial sutures do not transect the lateral margins of the frontal lobe.

Thorax. Although complete thoraxes have not been found, it is certain that they comprise 11 segments as in all other calmoniids. The axis is moderately convex, about one-third of the thoracic width, with each ring sagittally constricted and bearing a prominent but rather short median spine, on either side of which is a small tubercle. The axial rings broaden distally and are separated by pronounced ring furrows with distal apodemal pits. The pleurae have distinct fulcra and are divided into anterior and posterior moieties by deep, rather broad pleural grooves. The pleurae have short, posteriorly directed distal spines and are separated by well-defined, narrow interpleural grooves. At the fulcral axis, the posterior moiety of each pleura develops a fulcral spine of variable prominence, in some individuals almost as long as the axial spines (Fig. 97A), whereas in others (Fig. 103) they are little more than tubercles. The posterior moieties are also ornamented with a small tubercle immediately adaxial to the fulcral spine, as well as 2–4 variably developed tubercles abaxial to the fulcral spines.

Pygidium. The pygidium is moderately convex, subtrigonal in outline, and wider than the sagittal length (if the length of the rather prominent post-axial spine is excluded). The axis is rather broad anteriorly but tapers posteriorly to terminate rather indistinctly in a bluntly rounded tip. There are 8 distinct axial rings, narrower than the ring furrows, with a very indistinct ninth ring to the posterior. On the best-preserved pygidium (Fig. 102C–E), distinct median tubercles can be seen on the second, third and fifth rings, while the fourth, sixth and seventh rings are crenulated by a transverse row of weak, tiny tubercles. There is a well-developed post-axial field that is extended into a long, subcylindrical spine tilted upward (dorsally) somewhat. The pleural fields are rather convex, subtrigonal in outline and comprise 5 pairs of pleurae, of which the posterior pair are small and reduced. There are deep, rather broad pleural grooves and fine, indistinct interpleural furrows. The posterior moieties, which are thicker and more pronounced than those to the anterior, bear transverse rows of 2–4 tiny tubercles. The segmentation becomes obsolete distally so as to leave a more or less smooth border. However, the pygidial margin is marked by 5 pairs of denticles that are situated opposite the pleural 'ribs' and give the margin a scalloped appearance.

Discussion

Rennie (1930) felt that *B. arbuteus* and *B. cristagalli* (Woodward) might have been created for different parts of the same animal. However, material in

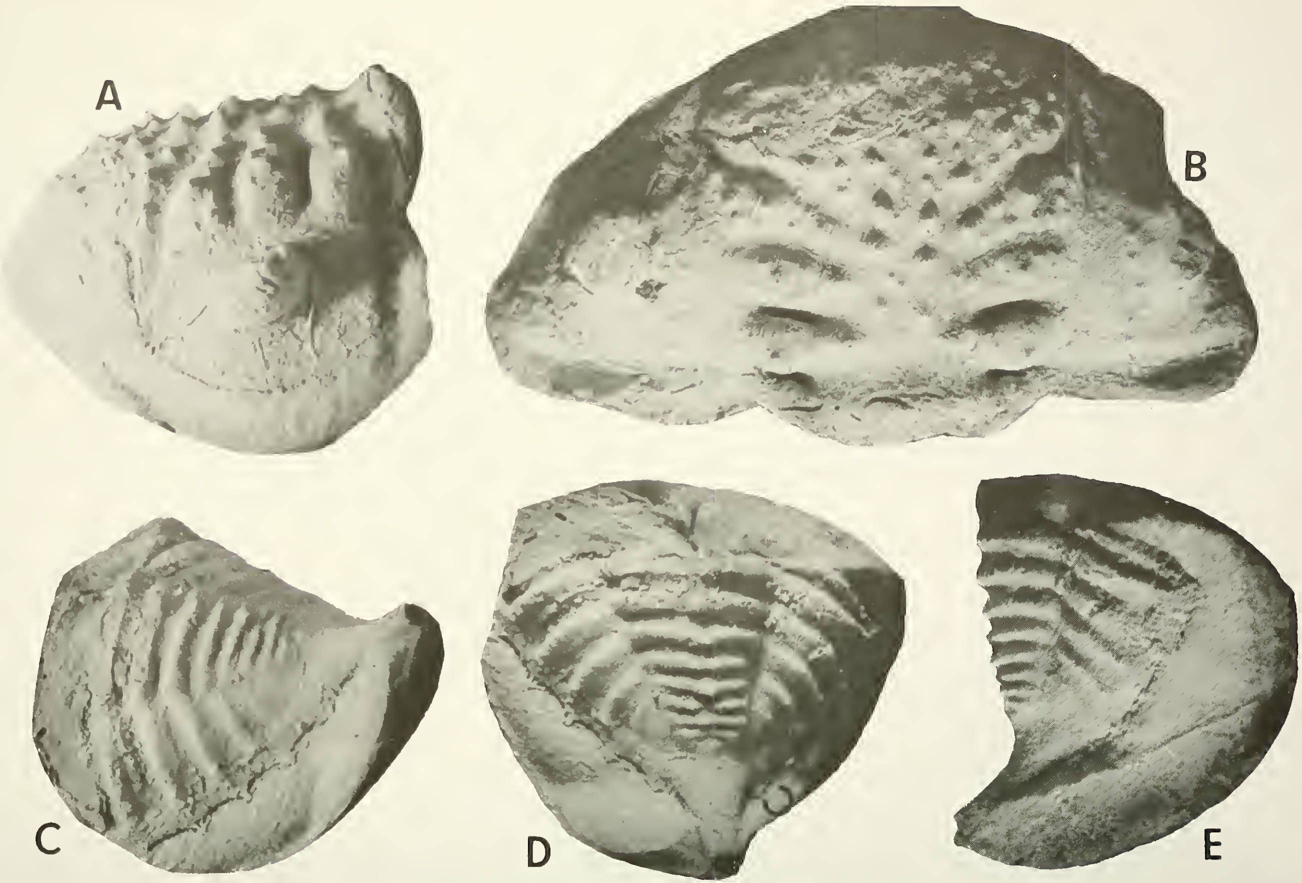

Fig. 102. *Bainella arbuteus* (Lake). A–B. RO–707. C–E. RO–298. Note the weak, irregular axial tubercles, marginal denticles and cylindrical terminal spine. Both preserved as internal moulds and both × 1,5.

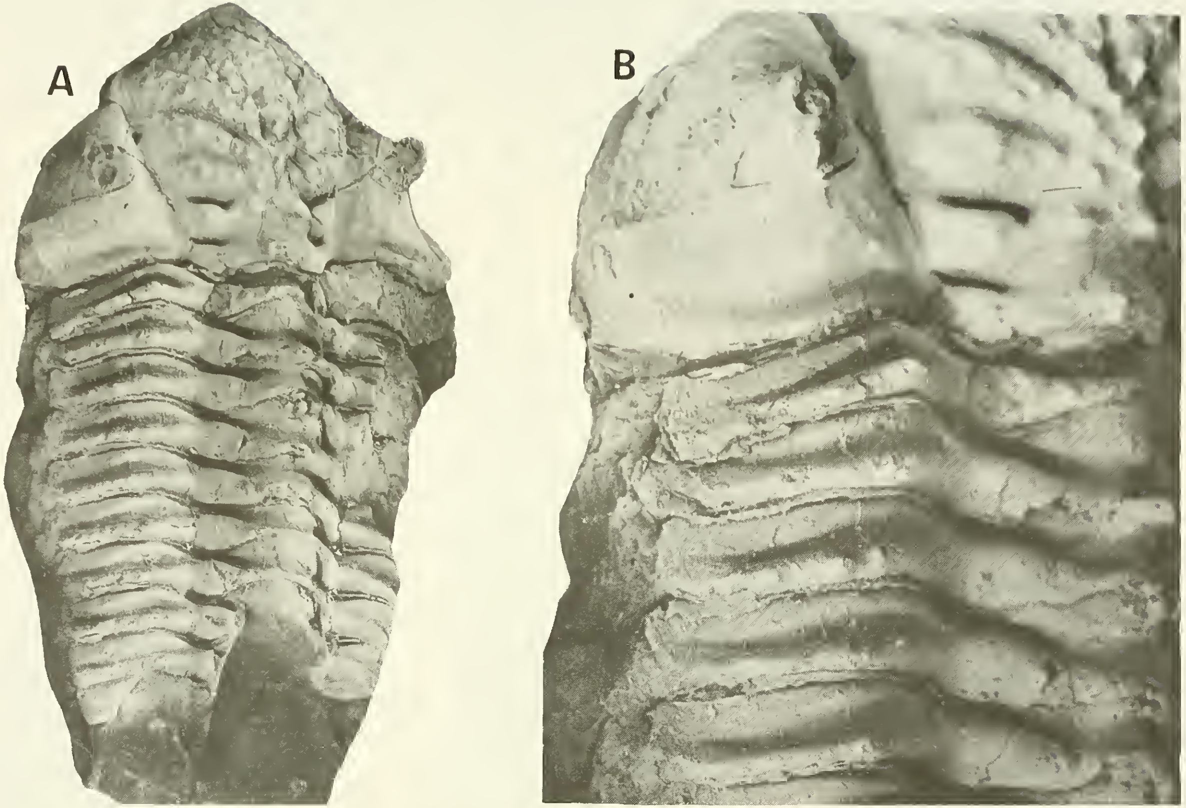

Fig. 103. *Bainella arbuteus* (Lake). RO–C72, preserved as an internal mould. A. × 1. B. Showing details of the pleural tuberculation. × 2.

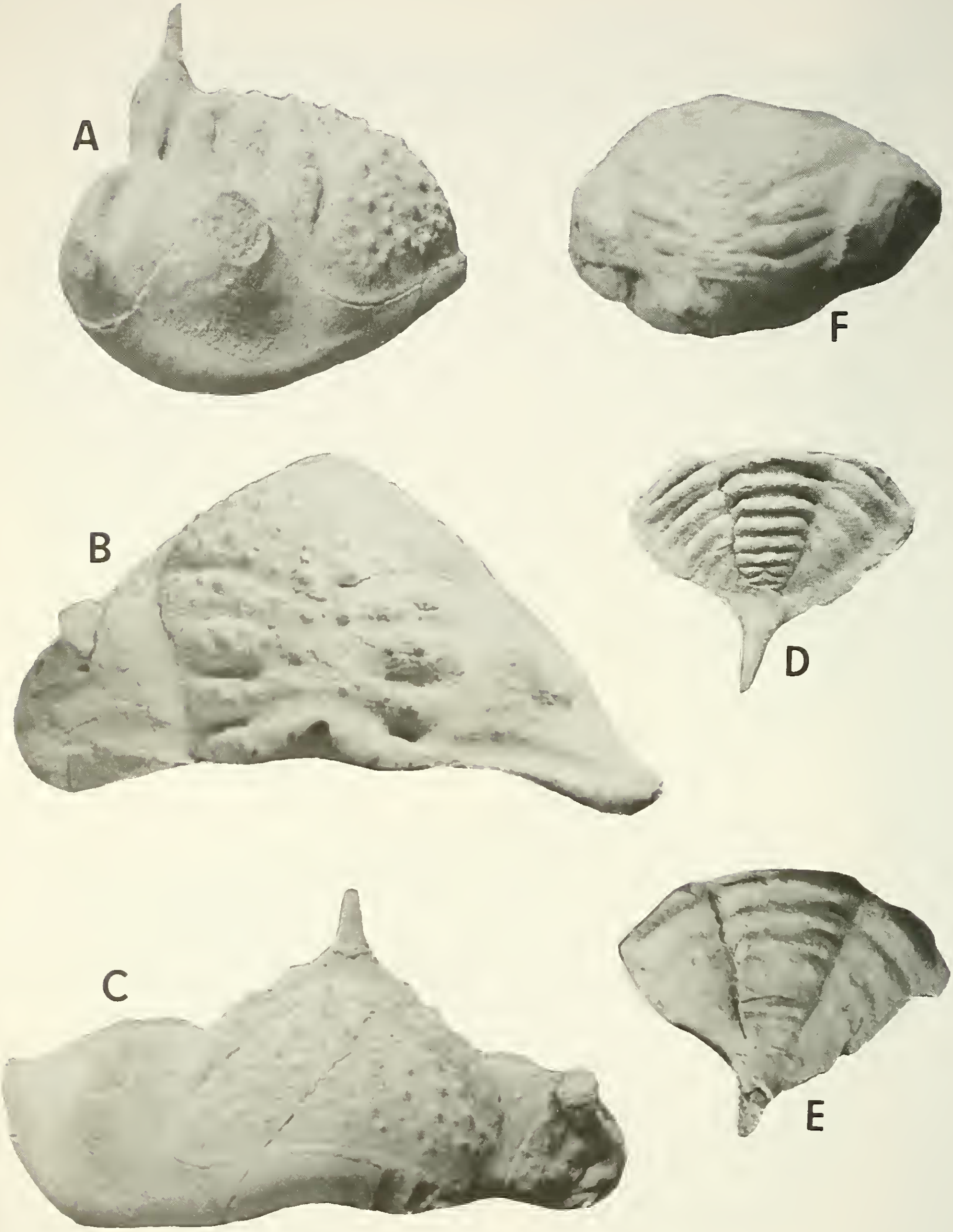

Fig. 104. A–E. *Bainella arbuteus* (Lake). A–C. RO–24. Note the prominent spine bases at the genal angles. × 1,5. D. RO–805, latex cast of an external mould. × 1. E. RO–805, the internal mould. × 1. F. *Bainella cristagalli* (Woodward). RO–160, an unusually large cephalon preserved as an internal mould. × 1.

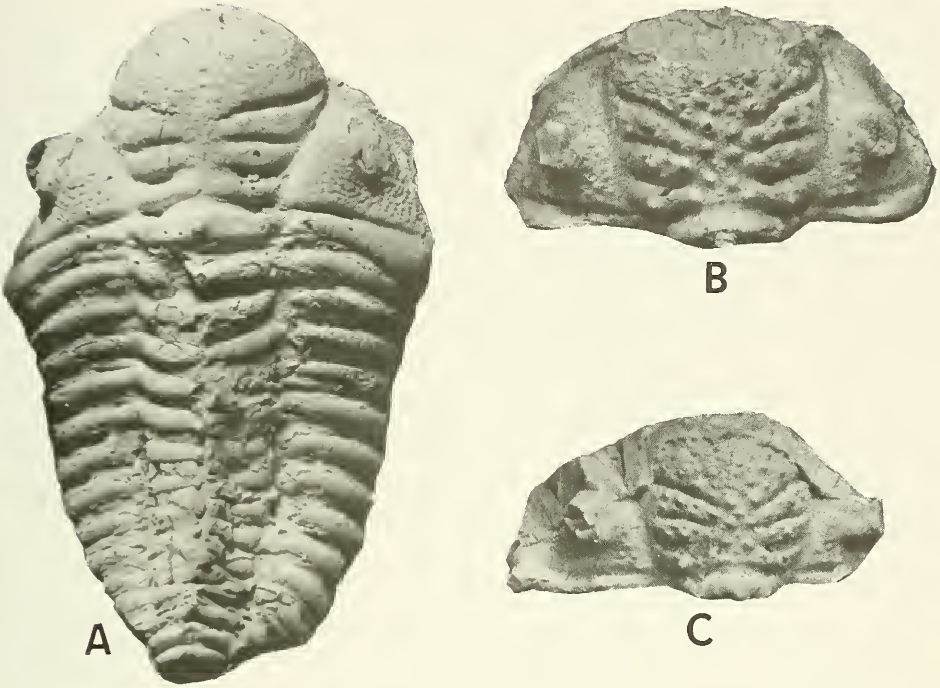

Fig. 105. A. *Bainella gamkaensis* Rennie. RO–67, a relatively complete example retaining cuticle. B–C. *Bainella arbuteus* (Lake). Latex casts of external moulds. B. RO–707 (see also Fig. 102A–B). C. RO–24 (see also Fig. 104A–C). All × 1.

the collection of R. Oosthuizen shows them to be readily separable morphologically although there is a difficult-to-prove possibility that they may be sexual dimorphs. The available material is certainly inadequate to establish the latter possibility and it is not pursued further here.

Bainella cristagalli (Woodward) (Fig. 106) differs from *B. arbuteus* by the finer, more regular tuberculation of its cephalon, the presence of up to 3 tubercles on either side of the sagittal spines on the axial rings, the absence of fulcral spines, its smaller size, and the presence of more pronounced median tubercles and transverse tuberculation to the axial rings of the pygidium of *B. arbuteus*.

The specimen figured by Reed (1925*a*) (Fig. 44B) as perhaps the pygidium of *Phacops (Phacopina) hiemalis* seems to be based upon a pygidium of *B. arbuteus* that has lost the terminal spine.

Metacryphaeus boulei (Kozlowski) bears a remarkable homoeomorphic resemblance to this species in features of the cephalon, but lacks axial and fulcral spines, as well as a terminal spine to the pygidium.

In features of the cephalon, such as sinuous 3p furrows, deeply incised glabellar segmentation and form of the genal angles, *B. sanjuanina* Baldis closely approaches *B. arbuteus*, differing almost solely in having the cephalon pitted (on the internal mould) rather than tuberculate. *Bainella arbuteus* is also allied to *B. insolita* (Wolfart) in regard to characters of the pygidium and the possession of short sagittal spines, but the two species are readily separated on cephalic features.

Occurrence

Bainella arbuteus (Lake) is currently known only from the Gydo Formation of the Bokkeveld sequence.

Bainella cristagalli (Woodward, 1873)

Figs 5D, 65A, 97I–J, 104F, 106–109

Encrinurus cristagalli Woodward, 1873: 31, pl. 2 (figs 6–7).
Phacops arbuteus Lake, 1904: 203, pl. 24 (fig. 3 only).
Non Phacops crista-galli (Woodward) Lake, 1904: 205, pl. 24 (fig. 5) (= *B. africana*).
Phacops crista-galli (Woodward) Schwarz, 1906: 392, pl. 10 (fig. 6).
Bainella sp., Rennie, 1930: 354, pl. 9 (fig. 18).

Material

The holotype (Fig. 107), by monotypy, in the British Museum, together with SAM–7178, 8976, 9606, AM–5, and RO–38, 66, 160, 224, 709, 747, 751, 763, 788–790, 806, C77, and E62.

Description

Cephalon. The cephalon is subtrigonal in dorsal outline, moderately convex, and about twice as wide as the sagittal length. The glabella is moderately inflated, subpentagonal in outline, with well-marked segmentation and a rhomboidal frontal lobe. The axial furrows are broad and shallow and diverge slightly to the anterior. The 3p furrows are fairly deep, slightly sinuous and directed posteromedially; the 2p furrows are of similar depth, transverse to slightly convex anteriorly, and connect weakly with the axial furrows; the 1p furrows are anteriorly concave, with deep linear apodemal pits adaxially, and weakly confluent with the axial furrows. The L1 lobes are rather narrow (exsag.) when compared with the other lobes. The occipital furrow is bowed forward sagittally, with deep apodemal pits distally. The occipital ring is of constant width, with a long median spine that distally curves slightly to the posterior and is flanked on either side by 2–3 small tubercles. The whole of the glabella is covered with small, apparently randomly distributed, tubercles of more or less even size. The cheeks are subtrigonal, weakly convex, with the genal angles produced into stout, diagonally directed spines whose distal terminations are unknown. The posterior border furrows are rather deep and well defined, meeting the shallower, indistinct lateral border furrows in acute angles. The posterior borders broaden (exsag.) towards the genal angles and carry a transverse row of small tubercles. The rather large eyes, more than

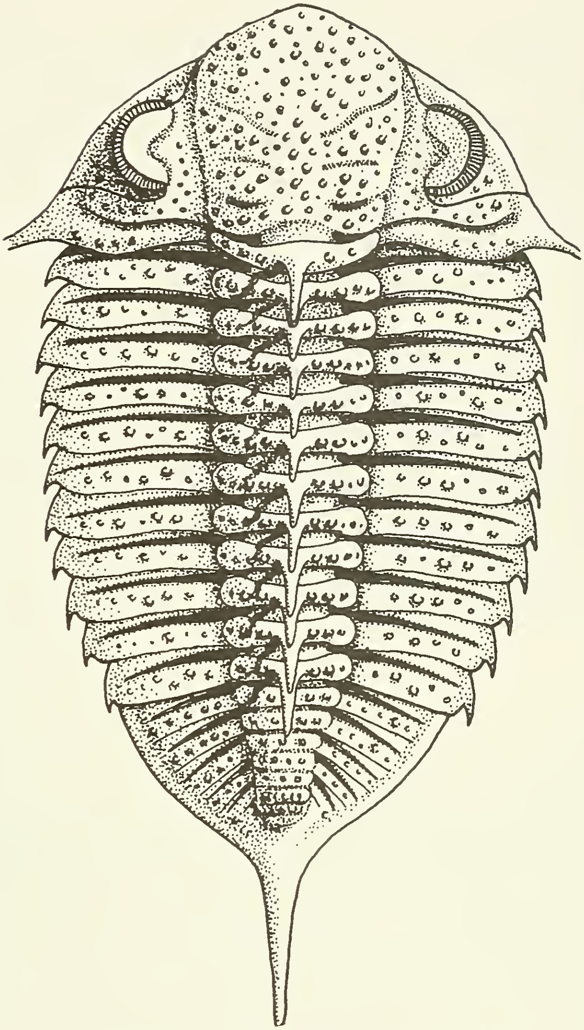

Fig. 106. *Bainella cristagalli* (Woodward).
A reconstruction based upon the available material.
×2.

one-third of the exsagittal length, are situated on palpebral prominences and comprise 28–30 vertical files, with up to 8 ocelli per file. There are small, scattered tubercles both on the fixigenae and librigenae; this tubercle development is noteworthy between the eyes and the axial furrows and there is a transverse row of tubercles on the fixigenae just anterior to the posterior border furrow.

Thorax. The thorax has a rather broad, moderately convex axis that is about one-third the thoracic width. All axial rings are slightly constricted sagittally and ornamented with prominent, long median spines; on either side of the latter on the axial rings are generally 2 prominent tubercles and a variable number, from 2–5, of smaller tubercles. The ring furrows are prominent, with distal apodemal pits. Each pleura has a distinct fulcrum and a deep pleural groove that separates a narrow (exsag.) anterior moiety and a prominent, relatively much broader, posterior moiety; the latter is ornamented with a transverse row of 5–7 small, distinct tubercles.

Pygidium. The pygidium is moderately convex, subtrigonal in dorsal outline, and distinctly wider than the sagittal length if the terminal spine is excluded. The axis is strongly convex, with pronounced axial furrows that converge only slightly to the posterior, and terminates in an indistinct, bluntly rounded tip. There are 8 axial rings, much wider than the ring furrows, with the last ring weak and indistinct in some individuals (Fig. 109). The rings are ornamented with transverse rows of up to 5 small tubercles that, on RO–790 (Fig. 109), give the sixth and seventh rings a crenulated appearance. The pleural fields are ornamented with 4 pairs of prominent ribs, each of which bears a transverse row of up to 5 tubercles, and a weakly developed fifth pair to the posterior. The ribs become obsolete distally, leaving a narrow, smooth border which seemingly lacks the marginal denticles of *B. arbuteus*.

Discussion

Differences from other species of *Bainella* have been noted above. The small size and relatively large eyes of *B. cristagalli*, together with similarities in

Fig. 107. *Bainella cristagalli* (Woodward). The holotype, by monotypy, and original of Woodward (1873, pl. 2 (figs 6–7)), which seems to retain cuticle; housed in the British Museum (Natural History). × 1,5.

glabellar segmentation, tubercle distribution and the form of the genal angles when compared with *B. arbuteus* give the writer the impression that one is dealing here with sexual dimorphs. Since available evidence is insufficient to establish this, they are treated as morphologically distinct but closely allied species.

As noted by Rennie (1930), this species closely resembles *Malvinella haugi* (Kozlowski) (1923: 51, pl. 2 (figs 11–14); Wolfart 1968: 107, pl. 18 (figs 2–4), pl. 19, pl. 20 (fig. 1)) in cephalic features, but the Bolivian species lacks axial

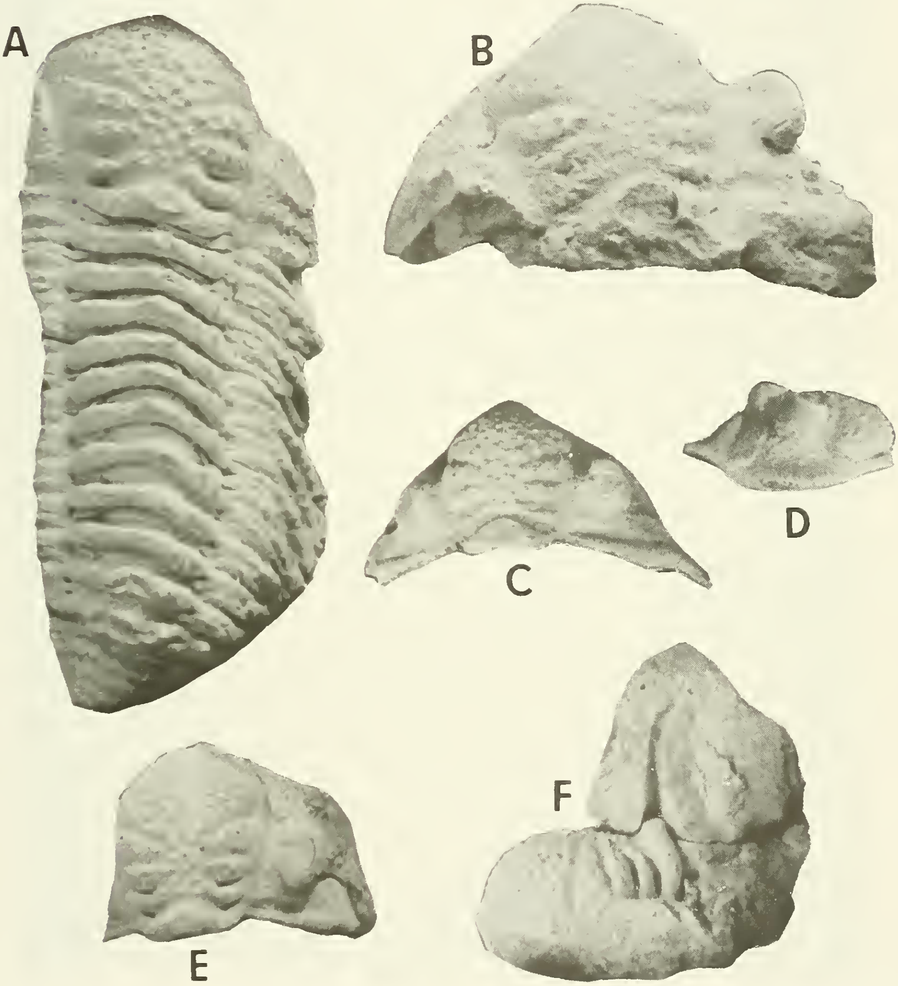

Fig. 108. *Bainella cristagalli* (Woodward). A. RO–747. × 1,5. B. RO–788. × 1,6. C–D. RO–751. × 1,4. E–F. RO–38. × 1,6. All preserved as internal moulds.

Fig. 109. *Bainella cristagalli* (Woodward). RO–790, an internal mould. (See also Fig. 97I.) ×5.8.

spines and a terminal spine to the pygidium. Again, the similarities seem to be due to convergence.

Occurrence

Bainella cristagalli (Woodward) is at present a South African endemic, known only from the Gydo Formation of the Bokkeveld Group.

Bainella gamkaensis Rennie, 1930

Figs 44C, 87B, 105A, 110–112

? Phacops (Bouleia?) sharpei Reed, 1925*a*: 161, pl. 9 (fig. 6), pl. 10 (fig. 9).
Bainella gamkaensis Rennie, 1930: 353, pl. 9 (figs 14–17).
Bainella (Belenops) gamkaensis Rennie, Eldredge & Braniša, 1980: 204.

Material

The holotype, SAM–8977, together with RO–37, 67, 750, 792, 795, C71, BPI–i248, 250, and questionably the lectotype, designated herein, of *P. (Bouleia?) sharpei* Reed, SAM–7794.

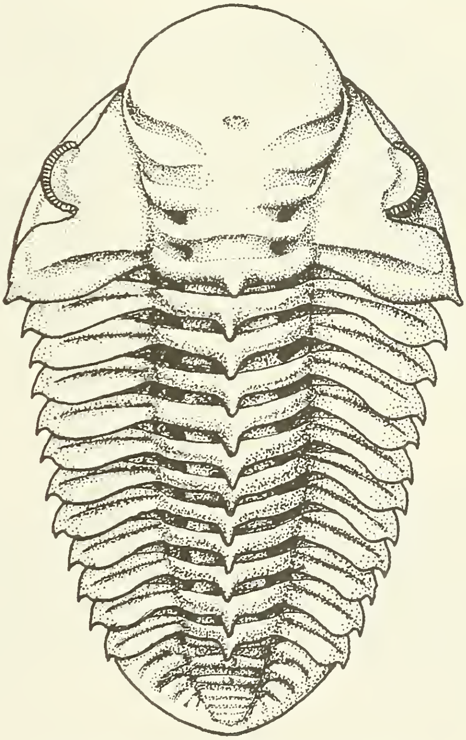

Fig. 110. *Bainella gamkaensis* Renni.
A reconstruction based upon the available material.
×1.

Description

Cephalon. The cephalon is much wider than the sagittal length, semicircular and rather convex. The glabella is expanded forward, with well-defined axial furrows and an inflated frontal lobe that overhangs the anterior border. There is a distinct posterior median pit to the frontal lobe but no well-developed auxiliary impression system. On internal moulds, the 3p furrows are broad (exsag.), sinuous, almost connecting with the 2p furrows proximally but failing to unite with the axial furrows. The 2p furrows are also very broad (exsag.), transverse, and weakly connected to the axial furrows. The 1p furrows are broad (exsag.), transverse, with deep apodemal pits adaxially, and strongly connected to the axial furrows. When the cuticle is preserved (Fig. 105A), the glabellar furrows are somewhat narrower (exsag.) and the 2p and 3p furrows remain well separated proximally. On internal moulds the L1 lobes are very narrow (Fig. 111), being very much broader when the cuticle is preserved. The rather broad occipital furrow, especially on internal moulds, is bowed forwards slightly sagittally and with deep apodemal pits distally. The occipital ring is of more or less uniform width and bears a short median spine. The 'drooping' cheeks are curved strongly downward, subtrigonal in outline, and with the eyes elevated on large palpebral prominences. The posterior border furrows are deeply incised, transverse, while the posterior borders broaden (exsag.) markedly towards the genal angles. The latter are acutely rounded and bear short genal spines. The lateral border furrows are shallow and indistinct. The eyes are well separated from the glabella and lie well below the level of the median glabellar area. The ocelli are arranged in vertical files, but the number of lenses per row is difficult to ascertain, probably about 8–9 in the central files. As in *B. africana*, there are distinct eye ridges. The anterior branches of the facial sutures *do not* transect the lateral margins of the frontal lobe, while the posterior branches pass almost straight outwards to meet the lateral margins opposite the posterior ends of the eyes. The base of the frontal lobe is carinate-bisulcate, the upper groove representing a preglabellar furrow and the lower groove the anterior border furrow. The intervening ridge marks the line of the rostral suture. On internal moulds the surface of the cephalon is distinctly granulose, whereas the cuticle (Fig. 44C) is very finely granulose and prominently dimpled.

Thorax. The thorax of *B. gamkaensis* cannot readily be distinguished from that of *B. africana* although, where observed, the axial spines seem to be significantly shorter and stubbier. The axial rings are constricted sagittally and broaden distally, and are separated by deep ring furrows. The axis is about one-third the thoracic width. The pleural fields are moderately convex, with deep pleural grooves and well-defined interpleural furrows. The posterior moiety of each pleura is much broader (exsag.) and more inflated than the anterior moiety.

Pygidium. The pygidium is almost semicircular in outline, wider than the sagittal length, and moderately convex. The axis is rather broad anteriorly and

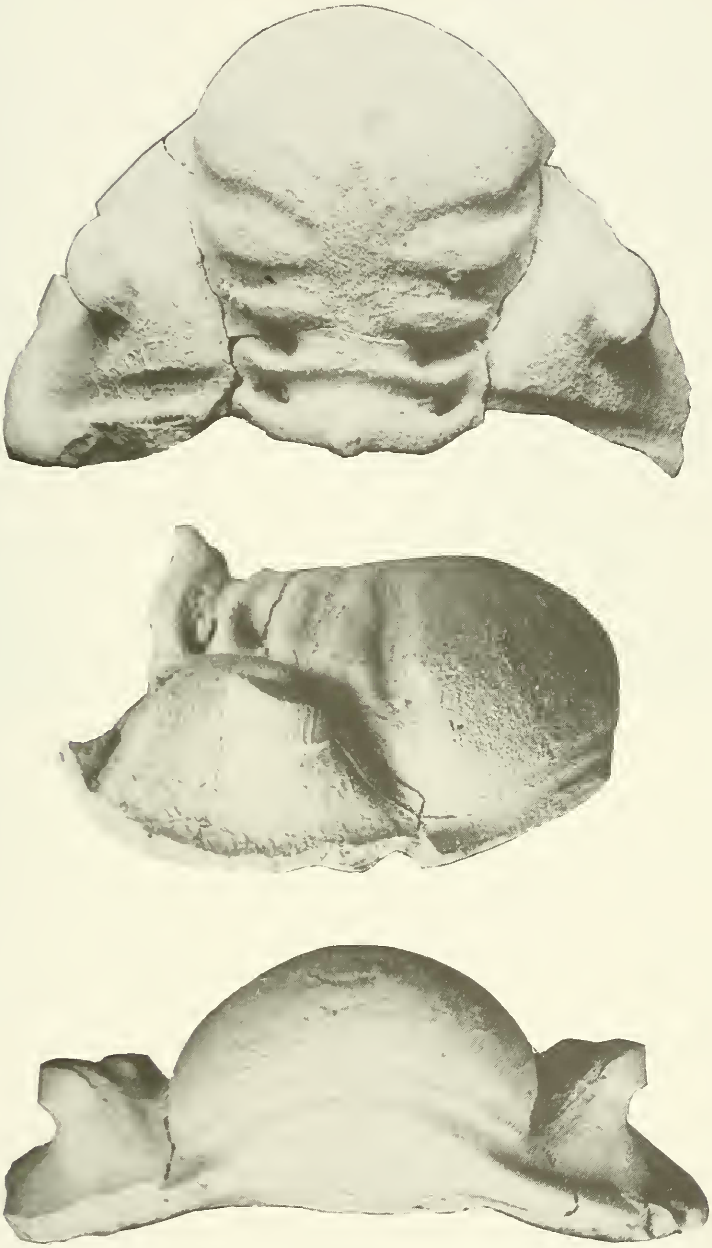

Fig. 111. *Bainella gamkaensis* Rennie. SAM–8977, the holotype, an internal mould figured by Rennie (1930, pl. 9 (figs 14–16)). × 1,6.

Fig. 112. *Bainella gamkaensis* Rennie. RO–37, a pygidium retaining cuticle. × 6.

tapers to the posterior to terminate in a truncate, indistinct tip a short distance inside the pygidial margin, leaving a short post-axial field. The axis comprises 7 distinct rings, of which the anterior 3 are narrower than the ring furrows and bear a well-developed median tubercle. The pleural fields are moderately convex, subtrigonal in outline, and ornamented with 4 prominent pairs of ribs, with a very reduced fifth pair to the posterior. The ribs are about as wide as the intervening grooves and terminate a short distance inside the pygidial margin so as to leave a narrow, smooth border. The entire surface of the pygidium is finely granulose.

Discussion

Phacops (Bouleia?) sharpei Reed was based upon isolated pygidia that compare very favourably with *B. gamkaensis* except that in the lectotype (Fig. 87B), preserved as an internal mould, the writer was unable to discern the small median tubercles on the anterior 3 rings that are found on the exoskeleton of *B. gamkaensis*. While this may merely reflect the different types of preservation, the writer is loath to replace Rennie's well-established name by the poorly known *Ph. sharpei*, and Reed's name is herein considered both a *nomen dubium* and a *nomen oblitum*.

As noted by Eldredge & Braniša (1980), the closest relative of *B. gamkaensis* is undoubtedly *B. insolita* (Wolfart) (1968: 113, pl. 21 (figs 2–3); Eldredge & Braniša 1980: 204, figs 21, 6–9) which differs in having a less inflated frontal lobe, less deeply incised 2p and 3p furrows, somewhat smaller eyes, lacks an anterior border furrow and has a very different pygidium with prominent post-axial spine and sagittal tubercles on most of the rings. There are also many more pleurae to the pygidium, which terminate in marginal denticles. In view of its somewhat older age, there can be no doubt that *B. gamkaensis* was descended from *B. insolita*.

Occurrence

Bainella gamkaensis Rennie is currently recorded only from the Gydo Formation of the Bokkeveld sequence.

Bainella sp. nov.

Figs 37C–D, 113

Material

PEM–1200B and BPI–i244, both preserved as internal moulds.

Description

Cephalon. The cephalon is known only from specimen PEM–1200B in which it is not well preserved. Its transverse width was certainly greater than the sagittal length, probably with a subtrigonal dorsal profile. The glabella is moderately convex, with prominent axial furrows that diverge slightly to the anterior. The frontal lobe is rhomboidal but insufficiently well preserved to be certain of the presence or absence of ornament or an auxiliary impression system. The 3p furrows are deeply impressed, convex anteromedially, and directed strongly posteromedially, so as almost to meet sagittally. The 2p furrows are also well developed, anteriorly convex, and seem to join the axial furrows. The 1p furrows are very deep, anteriorly concave, and well connected to the axial furrows. L1 broadens (exsag.) distally whilst L2 narrows distally. L3 remains almost constant in width, perhaps broadening slightly distally. There is no evidence of tuberculation on any of the lobes or on the median area of the glabella. The occipital furrow is arched strongly forward sagittally and rather shallow, but with deep apodemal pits distally. The occipital ring is of constant width with the distinct base of a sagittal spine. The posterior border furrows are deep, subtransverse and there is a prominent posterior border. The genal angles are acute and might have tapered into genal spines. The cheeks are strongly downturned, but this feature is probably mostly due to lateral compression. The poorly preserved eye base suggests a moderately sized eye, perhaps about one-third of the exsagittal length of the cephalon. The facial sutures are not preserved.

Thorax. It is very similar to that of *B. africana*, typically damaged along the sagittal axis due to the breaking off of the sagittal spines. The ring furrows have prominent apodemal pits distally. The pleurae show a distinct fulcrum,

Fig. 113. *Bainella* sp. nov. PEM–1200B, a crushed internal mould. Note the strongly impressed 2p and 3p furrows, the non-tuberculate L2 and L3 lobes, and the short terminal spine to the pygidium. × 1.

much enhanced by crushing, with deeply impressed pleural grooves and weaker, narrower interpleural furrows.

Pygidium. The pygidium of PEM–1200B is poorly preserved. It is relatively rather large, trigonal, and produced posteriorly into a short, mucronate spine. The strongly convex axis comprises about 10 rings, while the pleural fields show 5 ribs, narrower than the interspaces, that weaken towards the seemingly entire border. BPI–i244 may be a well-preserved pygidium of this species. It is a strongly trigonal pygidium, wider than long (sag.), with a strongly convex axis comprising 10 rings. The anterior axial rings are narrower than the ring furrows but after the fourth ring they are broader (sag.) than the ring furrows. The anterior 3 ring furrows have well-developed apodemal pits distally. There is no post-axial field, the axial segmentation merely becomes obsolete and passes into a short, mucronate spine. The pleural fields are trigonal, strongly downturned, with 4 pairs of pronounced ribs, narrower than the interspaces, and a very weakly developed fifth pair to the posterior. Each rib bears a small but distinct node-like tubercle at the fulcrum axis. The ribs weaken towards the entire margin, becoming effaced just before they reach it. This specimen seems to retain much of its granular cuticle.

Discussion

There is no other species of *Bainella* with which the above material may reasonably be confused. It is closest to *B. sanjuanina* Baldis (1967: 791, pl. 1 (figs 1–4)), but the latter species has distinctly sinuous 3p glabellar furrows. It is clear that the above material represents a new species but, until better preserved material is forthcoming, the writer hesitates to name it.

Occurrence

Bainella sp. nov. is known only from the Bokkeveld Group; its state of preservation suggests the Gydo Formation.

Genus *Kozlowskiaspis* Braniša & Vaněk, 1973

Type species *Kozlowskiaspis superna* Braniša & Vaněk, 1973;
by original designation

Discussion

Eldredge & Braniša (1980) would recognize two stratigraphically separated subgenera within *Kozlowskiaspis*, the younger nominate subgenus and the older *K. (Romanops)* (= *K. (Romaniella)* Eldredge & Braniša (*in* Eldredge & Ormiston 1979), a *nomen nudum*). *Kozlowskiaspis (Romanops)* was distinguished by its narrower, more highly arched cephalon, narrower frontal lobe, narrower and more steeply sloping genae, flat cephalic borders that are not reflected down as in the nominate subgenus, and in pygidial characters. The latter include 8 (not 9) pairs of pleurae, minute nodes on the pygidial margin adjacent to the anterior 2 pairs of pleurae, a short post-axial field with a less highly emarginate posterior margin, and a narrower ventral doublure.

Kozlowskiaspis (Kozlowskiaspis) ceres (Schwarz, 1906)

Figs 114–115, 116E

Phacops (Cryphaeus) ceres Schwarz, 1906: 394, pl. 10 (fig. 1).
? Dalmanites (Acastella?) pseudoconvexus Reed, 1925*a*: 137, pl. 9 (fig. 8).
Dalmanites (Cryphaeus?) ceres Schwarz, Reed, 1925*a*: 148.
Dalmanites (Metacryphaeus?) ceres (Schwarz) Rennie, 1930: 336, pl. 9 (figs 1–2).

Material

The holotype, AM–67, the paratype, AM–27, together with AM–71, SAM–PDB5979, 11916, RO–84, and 755, all preserved as internal moulds.

Description

Cephalon. The cephalon is subtrigonal in outline, much wider than the sagittal length, and only weakly convex. The glabella is distinctly pentagonal, with weakly impressed, broad, shallow, almost parallel axial furrows and a rhomboidal frontal lobe. The latter is weakly convex, distinctly marked by the auxiliary impression system, and extends laterally to in front of the eyes, so that the anterior branches of the facial suture transect the lateral portions of the frontal lobe. The anterior border is very narrow with a very weak median rostrum. The 3p furrows are rather shallow, inclined posteromedially at about 50–60° to the axial furrows, and do not seem to connect with the axial furrows, which they approach very closely. The 2p furrows are transverse, slightly deeper than the 1p furrows, and distally obsolete so that the L2 and L3 lobes coalesce abaxially. The 1p furrows are transverse, with deep, linear apodemal pits and distinctly connected to the axial furrows. There is a weak but distinct sagittal ridge in AM–71, behind the frontal lobe. The occipital furrow is arched

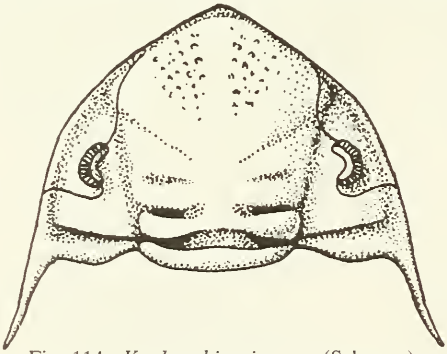

Fig. 114. *Kozlowskiaspis ceres* (Schwarz). A reconstruction based upon the available material. × 1,5.

strongly forward, of almost uniform width, and with deep apodemal pits abaxially. The strong arching of the occipital furrow results in a very significant broadening of the L1 lobes abaxially. The occipital ring is of constant width and lacks tuberculation. The cheeks are subtrigonal in outline and slope strongly downward. The posterior border furrows are deep and transverse, whereas the lateral border furrows are broad, shallow and indistinct. Anteriorly the border furrow is obsolete and the short median frontal process is separated from the glabella by a shallow preglabellar furrow. When preserved, the genal angles are produced into long, thin, posteriorly directed spines that curve inward distally, in some individuals at least. The eyes are small, less than one-third of the exsagittal cephalic length and somewhat elevated on palpebral lobes.

Thorax. Unknown.

Pygidium. On the ventral surface of the paratype cephalon, AM–27, is the internal mould of a pygidium unlike any other currently recorded from the

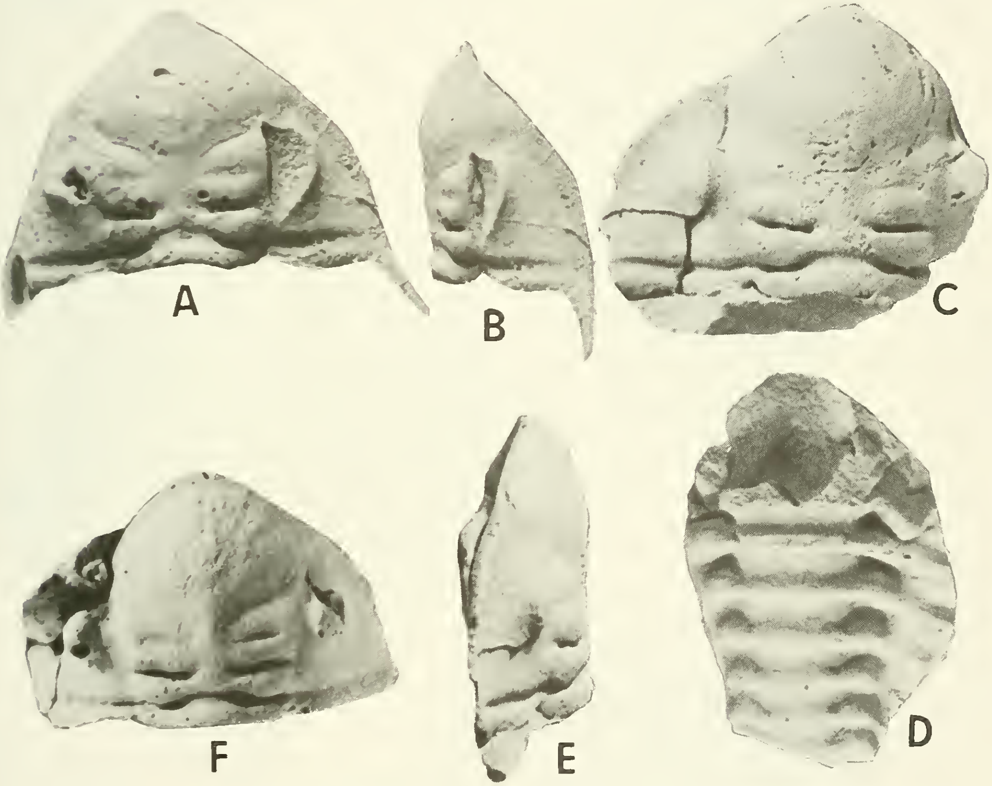

Fig. 115. *Kozlowskiaspis ceres* (Schwarz). A–B. AM–71. C–E. AM–27, the paratype cephalon with weakly impressed 2p and 3p furrows, and the pygidial fragment preserved on its reverse side. F. AM–67, the holotype figured by Rennie (1930, pl. 9 (figs 1–2)). Note the moderately impressed 2p and 3p furrows and the distinct auxiliary impression system. All preserved as internal moulds and all × 1,7.

Bokkeveld sequence. The pygidium is large (macropygous) with a broad, strongly convex axis that tapers slowly to the posterior so that the axial furrows, anteriorly at least, are subparallel. The anterior 4 rings are much narrower than the ring furrows, whereafter the rings and ring furrows are of more or less equal width (sag.). The posterior part of the axis is not preserved and hence only 7 axial rings can be counted; the pygidium was certainly significantly larger. The anterior 2 ring furrows preserve apodemal pits distally. The pleural fields are not preserved.

Discussion

The Bokkeveld species closely approaches *Kozlowskiaspis superna* Braniša & Vaněk (1973: 100, pl. 5 (figs 1–7); Eldredge & Braniša 1980: 260, figs 20, 27–28, 29B). However, the Bolivian species has a relatively broader cephalon with a subpentagonal outline in dorsal view, slightly larger eyes that are closer to the glabella, and weak axial furrow pits. It is not known if *K. superna* possesses the long genal spines displayed by *K. ceres*.

Occurrence

Kozlowskiaspis ceres (Schwarz) is at present a South African endemic, known only from the Gydo Formation.

Genus *Deltacephalaspis* Eldredge & Braniša, 1980

Type species *D. comis* Eldredge & Braniša, 1980;
by original designation

Discussion

This genus was well treated by Eldredge & Braniša (1980) who distinguished two subgenera, the nominate subgenus and *D. (Prestalia)*. The latter subgenus was separated on the basis of its highly arched cephalon with uptilted median rostrum, shorter genal spines that arise well to the posterior of the facial suture, and its downturned cheeks and relatively larger eyes.

Deltacephalaspis pseudoconvexus (Reed, 1925)

Figs 6A, 116A–D

Dalmanites (Acastella?) pseudoconvexus Reed, 1925*a*: 138, pl. 9 (fig. 9 only).

Material

The cephalon on which Reed (1925*a*) largely based his description, KM–419, is lost (P. Beaumont, *in litt.* 1980). Consequently, his figured syntype pygidium, SAM–7201 (Fig. 6A), is herein selected as lectotype. There are two other pygidia, SAM–13295*a–b*, preserved on the same block, that also belong here.

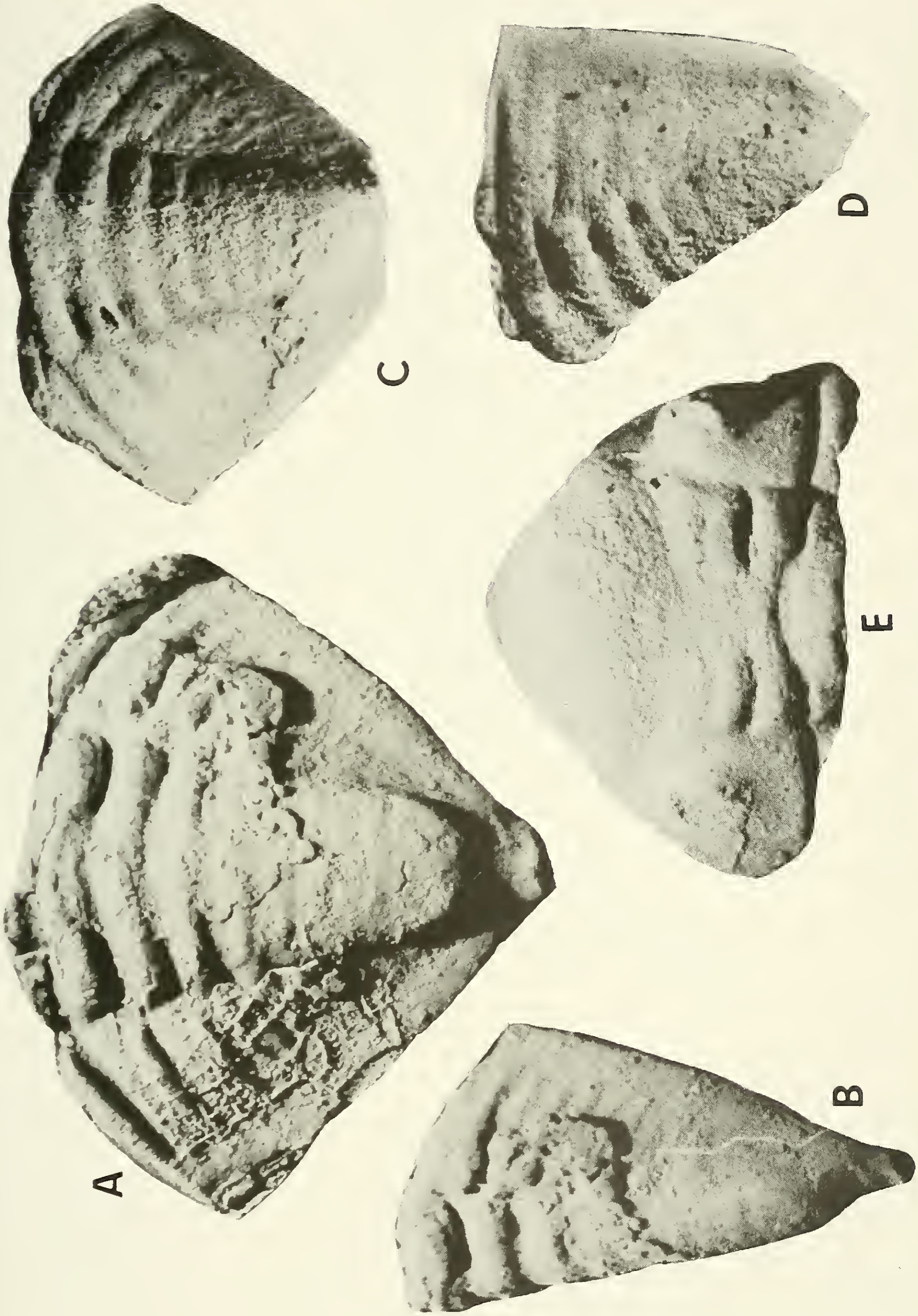

Fig. 116. A–D. *Deltacephalaspis pseudoconvexus* (Reed). A–B. SAM–13295a, × 4,1. C–D. SAM–13295b, × 4,1. E. *Kozlowskiaspis ceres* (Schwarz). SAM–11916. × 3,9.

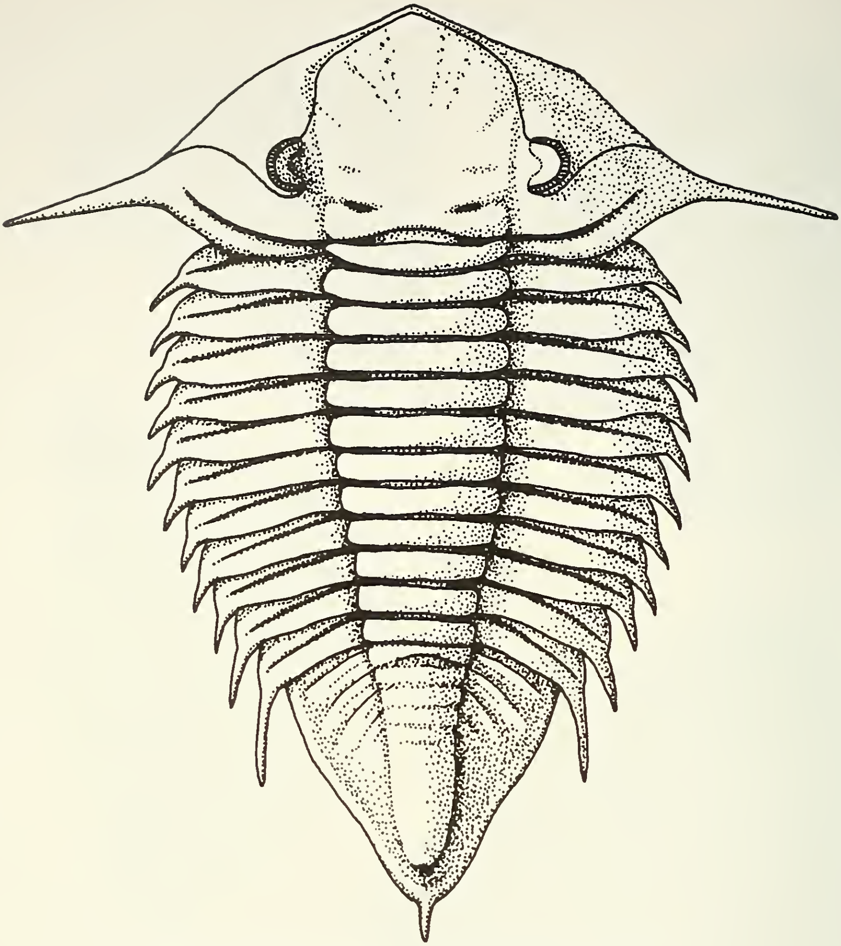

Fig. 117. *Deltacephalaspis magister* Eldredge & Braniša.
A reconstruction based upon the figured material.
× 2.

Description

The pygidium is strongly arched with a smooth, entire border and a well-developed, cylindrical terminal spine. The axis is weakly convex, broad anteriorly, and tapers rather rapidly to the posterior. It is bluntly terminated to the posterior, leaving a distinct post-axial field. Only the anterior 3 axial rings are well developed but, under good oblique lighting, a further 7 very faint and indistinct rings can also be discerned. The anterior 2 ring furrows bear apodemal pits distally. The pleural fields are triangular, weakly convex, sloping, with pleural segmentation obsolete after the third pair of pleurae. The pleural grooves are moderately deep and distinct, but become effaced distally to leave a rather broad, smooth border. The interpleural furrows are faint and indistinct.

Discussion

In the absence of cephala, the subgeneric assignment of *D. pseudoconvexus* is unknown. The pygidia of the Bokkeveld species are very close to those of *D. magister* Eldredge & Branisa (1980, fig. 13C–D) (Fig. 117 herein) but in the absence of more complete Bokkeveld material a detailed comparison is unwarranted. The pygidia of *D. comis* Eldredge & Branisa (1980, fig. 11F) and *D. retrospina* Eldredge & Branisa (1980, fig. 11G) possess variably developed axial tubercles, while the pygidia of species assigned to *D. (Prestalia)* are currently unknown.

Occurrence

Deltacephalaspis pseudoconvexus (Reed) is currently known only from the Gydo Formation of the Bokkeveld Group.

BIOSTRATIGRAPHY

Regional

Conventionally, the base of the Bokkeveld Group is drawn at the base of the first shale following conformably upon the white, uppermost quartzarenite of the Table Mountain Group. Theron (1970) envisaged deposition of the Bokkeveld succession in a shallow embayment open to the sea to the south-east, and flanked by mature, low-gradient coastal plains. The uniformity of the lower part of the Bokkeveld sequence, deposited at a time of peak transgression, contrasts strongly with the variability of the upper part, when major regression had set in. Consequently, the Bokkeveld sedimentary pile is divided into a lower Ceres Subgroup and an upper Bidouw Subgroup. Only the Ceres Subgroup and the Waboomberg Formation, the basal shale of the Bidouw Subgroup, have yielded marine invertebrates. The following lithostratigraphic subdivision of the marine part of the sequence has been recognized, from above downward:

(vii) Waboomberg Formation—fourth shale
(vi) Boplaas Formation—third sandstone
(v) Tra-Tra Formation—third shale
(iv) Hexrivier Formation—second sandstone
(iii) Voorstehoek Formation—second shale
(ii) Gamka Formation—first sandstone
(i) Gydo Formation—first shale

Schwarz (1906) was the first to make a determined effort to recognize a zonal succession within the Bokkeveld faunas, but without success. He noted, however, the prevalence of *Burmeisteria* in the western and northern outcrops (shallower, quieter waters?), spiriferids in the central region and calmoniid trilobites in the eastern outcrops. Theron (1972), on the other hand, noted some broad biostratigraphic subdivisions without doing any detailed palaeontological work; the Ceres Subgroup represents the *Australospirifer* Range Zone, the lower three formations the *Burmeisteria* Range Zone, the Hexrivier Formation the *Mutationella* Range Zone, and the contact horizon with the Table Mountain Group, between longitudes 20°45′ and 20°15′, a *Pleurothyrella* Range Zone. While Theron's (1972) attempt is admirable, it is clearly unsatisfactory and any serious biostratigraphic subdivision must await a modern revision of the invertebrate faunas.

So far as the trilobites are concerned, they are conspicuously rare in the sandstone units (high energy environments), which are dominated by the brachiopod *Australospirifer hawkinsi* (Morris & Sharpe), and hence are largely confined to the shale units. The vast majority of the trilobites come from the Gydo Formation, including *Bainella africana* (Salter), *B. arbuteus* (Lake), *B. cristagalli* (Woodward), *B. gamkaensis* Rennie, *Typhloniscus baini* Salter, *Renniella rossouwi* gen. et sp. nov., *Kozlowskiaspis ceres* (Schwarz), *Pennaia pupillus* (Lake), *Oosthuizenella ocellus* (Lake), *Deltacephalaspis pseudoconvexus* (Reed), *Francovichia clarkei* (Ulrich), *Ormistoniella malaca* (Lake), *Burmeisteria herscheli* (Murchison), *B. notica* (Clarke) and a *Metacryphaeus* sp. The only trilobites collected by the writer from the Voorstehoek Formation, or preserved in the soft greenish shales typical of this unit, are abundant *Metacryphaeus caffer* (Salter) and *Burmeisteria herscheli* (Murchison), together with *Gamonedaspis boehmi* (Knod), *Phacopina lakei* (Reed) and isolated examples of *Pennaia* sp. and *Ormistoniella malaca* (Lake). Although further collecting should amplify this list, it is clear that the trilobite faunas of these two units, and the relative abundance of the constituent species, are substantially different. It is proposed, therefore, to term the Gydo Formation the *Bainella africana* Assemblage Zone, and the Voorstehoek Formation the *Metacryphaeus caffer* Assemblage Zone. The writer has not seen trilobites from the Tra-Tra Formation, although Theron (1970) records *Burmeisteria herscheli* (Murchison) from this unit. The only trilobites so far recorded from the Waboomberg Formation are frequent *Metacryphaeus venustus* Wolfart and this unit accordingly becomes the *Metacryphaeus venustus* Assemblage Zone.

Interregional

The best stacked succession of Malvinokaffric trilobites is to be found in Bolivia where the following zonation may be recognized, somewhat modified from Wolfart (1968), from above downwards:

Cryphaeoides rostratus Assemblage Zone
Metacryphaeus tuberculatus Assemblage Zone
Metacryphaeus cornutus Assemblage Zone
Metacryphaeus giganteus Assemblage Zone
Bainella insolita Assemblage Zone

Since the writer would regard *Metacryphaeus tuberculatus* (Kozlowski) and *M. caffer* (Salter) as conspecific, these two zones should be regarded as strictly coeval and provide a direct biostratigraphic link between Bolivia and South

Africa. The general aspect of the faunas from the *Bainella africana* Assemblage Zone suggest an age somewhat younger than the *B. insolita* Assemblage Zone of Bolivia, as does the presence of *Metacryphaeus* and *Kozlowskiaspis (Kozlowskiaspis)* in the Gydo Formation. In addition, *Francovichia clarkei* (Ulrich) is very closely allied to *F. branisi* (Wolfart) and, on the basis of the available evidence, the writer would suggest a correlation of the *B. africana* Assemblage Zone with the Bolivian zone of *Metacryphaeus giganteus*. *Metacryphaeus venustus* Wolfart is relatively long-ranging, but its relative position in the South African sequence suggests a correlation with the Bolivian *Cryphaeoides rostratus* Assemblage Zone.

FAUNAL AFFINITIES

The Malvinokaffric Realm (Fig. 118) was predominant during the late Emsian and early Eifelian and shows a distinctive fauna characterized by very rare bryozoans and the absence of reef-building corals, graptolites, conodonts and goniatites, as well as by the diversity and abundance of calmoniid trilobites (which are seemingly restricted to this realm), bivalves, and a largely endemic suite of brachiopods from which atrypids and gypidulids are unknown. The absence of bedded limestones and reef-building corals, typical of this period in the Old World Realm, together with the general lack of diversity (at the family level), leaves little doubt that the Malvinokaffric Realm should be interpreted as comprising the shallow water, Arctic-type, epicontinental sea that flooded large areas of Gondwanaland (Clarke 1913; Grabert 1970; House *in* Middlemiss *et al.* 1971).

Antarctica

In this region Devonian strata are encountered in the Ohio Range of the eastern Horlick Mountains (Doumani *et al. in* Hadley 1965). Here, marine sandstones and shales of the Horlick Formation rest nonconformably upon granitic basement, thus clearly reflecting marine transgression, and have yielded a fauna that includes the brachiopods *Australospirifer*, *Cryptonella?*, *Tanerhynchia*, *Pleurothyrella*, *Orbiculoidea*, and *Lingula*, the trilobite *Burmeisteria*, the cricoconarid *Tentaculites*, and a number of bivalves and gastropods whose affinities lie with the Bokkeveld and South American faunas. While the brachiopod faunule displays similar affinities, '. . . the absence of key Malvinokaffric genera *Australocoelia*, *Scaphiocoelia* and *Notiochonetes* is unexplained' (Boucot *et al. in* Hadley 1965: 255). So far as the trilobites are concerned, the absence of calmoniids is noteworthy, while the 'Type II' pygidia of *B. antarctica* Saul seem closer to the New Zealand *B. expansa* (Hector) than to the Bokkeveld *B. herscheli*. Indeed, the faunas from the Horlick Formation seem to have closer links with Tasmania and New Zealand than with South Africa and, as such, do not support the direct marine link between South Africa and Antarctica so commonly shown on palaeobiogeographic maps. This provides

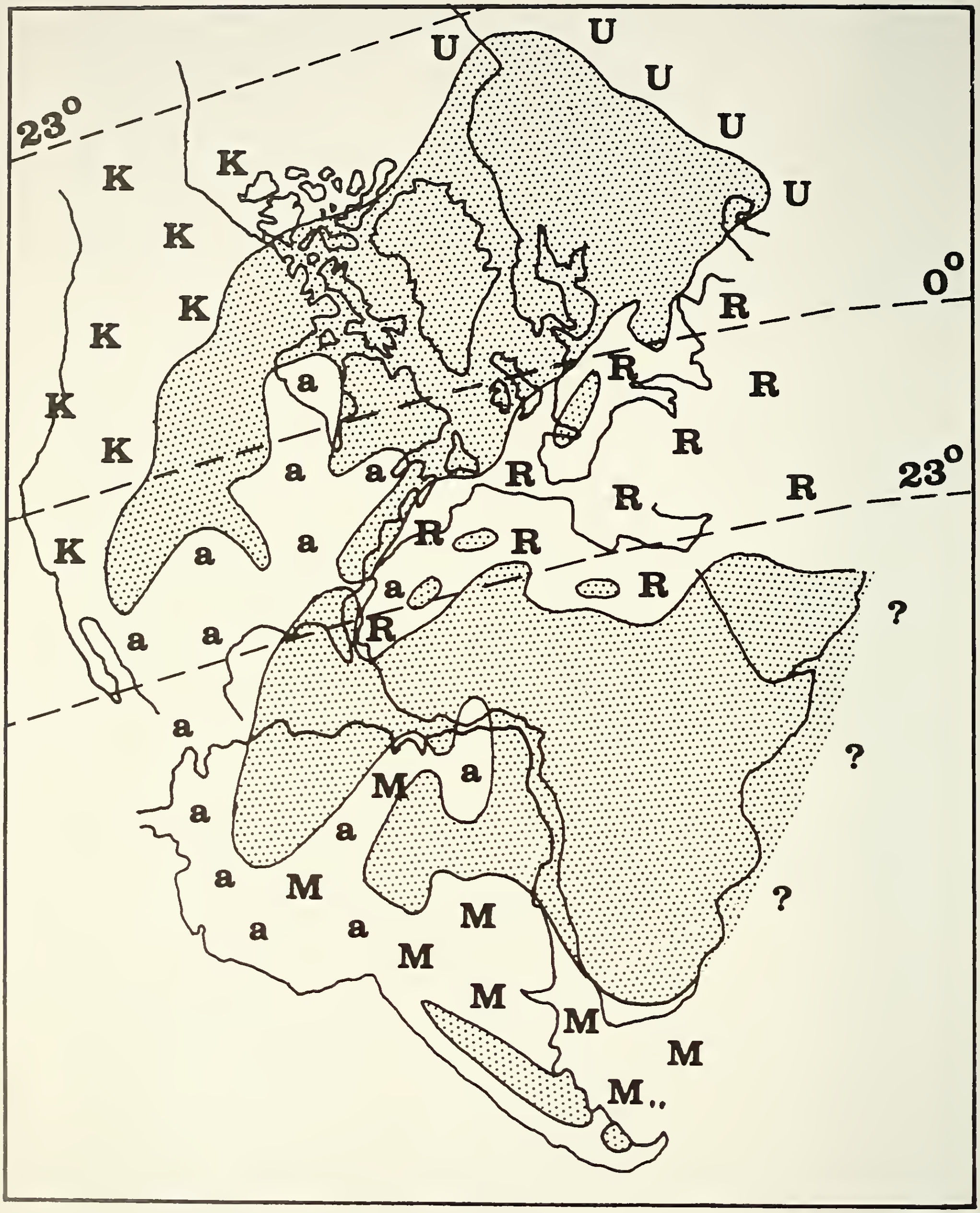

Fig. 118. Late Emsian–early Eifelian palaeobiogeography to show the extent of the Malvinokaffric Realm (M) with respect to the Old World Province. a = Appalachian Subprovince, K = Cordilleran Subprovince, U = Uralian Subprovince, R = Rhenish Subprovince, stippled areas = land.

some slight measure of support for the reassembly of Gondwanaland recently proposed by the writer (Cooper 1980), and it seems likely that migration between the epicontinental Malvinokaffric Realm and Antarctica occurred via an oceanic route the length of the west coast of South America.

As regards the age of the Horlick Formation, it is clearly Devonian but a more precise age is largely speculative. It seems reasonable, however, to assume contemporaneity with the Reefton Beds of New Zealand and hence an Emsian (late?) age.

Bolivia

The trilobite faunas from the Devonian of Bolivia are comparatively well known following the studies of Ulrich (1892, 1893), Knod (1908), Groth (1912), Kozlowski (1923), Swartz (1925), Braniša (1960, 1965), Wolfart (1968), Braniša & Vaněk (1973), and Eldredge & Braniša (1980). As outline above, the following biostratigraphic subdivisions of the Devonian in Bolivia may be recognized:

(v) *Cryphaeoides rostratus* Zone (= lower Sicasica Formation)—with the genera *Cryphaeoides*, *Metacryphaeus*, *Phacops (Viaphacops)*, and *Trimerus (Dipleura)*

(iv) *Metacryphaeus tuberculatus* Zone (= uppermost Belén Formation)—with *Metacryphaeus*, *Pennaia*, *Vogesina*, and *Acanthopyge*

(iii) *Metacryphaeus cornutus* Zone (= low Upper Belén Formation)—with the trilobites *Malimanaspis*, *Phacops (Viaphacops)*, *Bouleia*, *Metacryphaeus*, *Pennaia*, *Schizostylus*, *Vogesina*, *Malvinella*, and *Acanthopyge*

(ii) *Metacryphaeus giganteus* Zone (= upper Lower Belén Formation)—with *Boliviproetus*, *Phacops (Viaphacops)*, '*Australosutura*', *Francovichia*, *Fenestraspis*, *Chacomurus*, *Chiarumanipyge*, *K. (Kozlowskiaspis)*, *Bouleia*, *Vogesina*, *Malvinella*, *Metacryphaeus*, *Pennaia*, and *Schizostylus?*

(i) *Bainella insolita* Zone (= lowest Belén Formation and Gamoneda Formation)—yielding *Phacopina*, *Bainella*, *Deltacephalaspis (Deltacephalaspis)*, *D. (Prestalia)*, *Kozlowskiaspis (Romanops)*, *Pennaia*, *Tarijactinoides*, *Schizostylus (Curuyella)*, *Bouleia*, *Parabouleia*, *Gamonedaspis*, *Francovichia?*, *Otarion (Maurotarion)*, and *Burmeisteria*

As regards the chronostratigraphic correlation of these biostratigraphic units, it is noteworthy that *Phacops (Viaphacops)*, which first appears in the *M. giganteus* Zone, is typically a late Emsian/Eifelian taxon in the Appalachians and Siberia (N. Eldredge *in litt.*, 1980). Moreover, the presence of *Trimerus (Dipleura) dekayi* (Green) in the *Cryphaeoides rostratus* Zone, together with the brachiopod *Pustulatia pustulosa* (Hall), allows a direct tie with the Hamilton Group of the Appalachian Province and hence an Eifelian–Givetian age for this biostratigraphic unit. The correlation with the Bokkeveld faunas has already been noted.

Brazil

The trilobite faunas of Brazil have been recorded by Hartt & Rathbun (1875), Katzer (1903), and Clarke (1890, 1913) but are now urgently in need of modern revision.

The stratigraphy of the Amazonas Basin was discussed by Krömmelbein (1967), who recognized the following succession:

2. Curuá Formation
    (ii) Xingú Member—gray and greenish, silty, micaceous, or clayey shales
    (i) Barreirinha Member—black, fissile, euxinic shales

1. Maecurú Formation
    (ii) Ariramba Member—60–400 m of alternating sandstones and siltstones with interbedded dark gray, micaceous shales
    (i) Jatapú Sandstone—100–400 m of poorly cemented, whitish, fine-grained quartzarenite with locally interbedded grey to black siltstones and shales.

The Jatapú Sandstone has yielded abundant trace fossils only, while almost all the body fossils collected from the Amazon basin, including those described by Hartt & Rathbun (1875), Clarke (1890), and Katzer (1903), are from the Ariramba Member. However, according to Krömmelbein (1967), the latter unit may include more than one palaeontological horizon. The latter view is certainly supported by Krömmelbein's records of *Metacryphaeus* from this level, since the trilobite faunas described by Clarke (1890) reveal a very different aspect to those from the Bokkeveld sequence. The presence of a peculiar suite of trilobites, dominated by *Malvinella*-like forms, including *Phacopina braziliensis* (Clarke), *Pennaia menurus* (Clarke), *Tarijactinoides acanthurus* (Clarke), *Malvinella goeldi* (Katzer), '*Phacops*' (gen. nov. or aff. *Malvinella*) *scirpeus* Clarke, '*Dalmanites*' (gen. nov. or aff. *Malvinella*) *gemellus* Clarke, '*D*'. (gen. nov. aff. *Malvinella*) *tumilobus* Clarke, '*D*'. (gen. nov. aff. *Malvinella*) *australis* Clarke, '*D*'. (gen. nov. aff. *Vogesina*) *galeus* Clarke, '*Phacops*' *pullinus* Clarke, '*P*'. *macropyge* Clarke, *Metacryphaeus ulrichi* (Katzer), *M. paituna* (Clarke), '*Dalmanites*' (gen. nov. aff. *Fenestraspis*) *maecurua* Clarke, and '*D*'. *infractus* Clarke suggests an age close to that of the Bokkeveld *Metacryphaeus caffer* Assemblage Zone. Certainly it has a younger aspect than the faunas of the Gydo Formation.

In the Paraná Basin to the south, the Ponta Grossa Shale has yielded *Burmeisteria notica* (Clarke), *Metacryphaeus australis* (Clarke), *Pennaia pauliana* Clarke, *Calmonia signifer* Clarke, *C. micrischia* Clarke, *C. subsevica* Clarke, *Paracalmonia pessulus* (Clarke), and *Gamonedaspis accola* (Clarke).

The association of *Gamonedaspis* and *Metacryphaeus* is a feature of the Voorstehoek Formation of the Bokkeveld sequence and suggests a correlation with the Ponta Grossa Shale of Brazil.

Argentina

The Devonian stratigraphy of Argentina has been described by Padula *et al.* (1967), while the trilobite faunas have been recorded by Thomas (1905), Baldis (1967, 1972), Baldis *et al.* (1976), and Baldis & Longobucco (1977*a*, 1977*b*).

In the Argentinian Precordillera, the Talacasto Formation has yielded *Bainella sanjuanina* (Baldis 1967), together with *Metacryphaeus*, '*Homalonotus*', and *Trimerus* (Padula *et al.* 1967). The *Bainella* is closely allied to *B. arbuteus* (Lake) and its association with *Metacryphaeus* suggests a correlation with the *Bainella africana* Zone of the Bokkeveld sequence. This is perhaps also the level of *Dalmanitoides drevermanni* (Thomas 1905). In the same region, the somewhat younger Chavela Formation has yielded *Phacops chavelai* Baldis & Longobucco, *Bouleia dagincourti* (Ulrich), *Cryphaeoides rostratus* (Kozlowski), *Punillaspis argentina* (Baldis), and *Acanthopyge balliviani* (Kozlowski). This is a typical *Cryphaeoides rostratus* Zone faunal assemblage.

Falkland Islands

A Malvinokaffric trilobite fauna is recorded (Clarke 1913) from the Fox Bay Formation and includes *Bainella* cf. *africana* (Salter) (= *D. (M.) acacia* Clarke), *Oosthuizenella* cf. *ocellus* (Lake), *Metacryphaeus falklandicus* (Clarke), *Schizostylus? allardyceae* (Clarke), and *Burmeisteria herscheli* (Murchison). The fauna suggests a direct correlation with the *B. africana* Zone of the Bokkeveld sequence (Fig. 119).

AGE OF THE BOKKEVELD FAUNAS

Since the Malvinokaffric Realm is characterized by the absence of graptolites, conodonts and goniatites, just these taxa that in the Old World Realm serve as prime stratigraphic indicators, the precise age of the Bokkeveld sequence has been largely a matter for speculation. Thus, Reed (1907) considered the Bokkeveld faunas to be most closely allied to those from the upper Lower Devonian (Coblenzian = Siegennian–Emsian) of western Europe and to the Middle Devonian (Hamiltonian) of North America. Du Toit (1954: 252) regarded the lower half of the Bokkeveld Group as '. . . *Lower* and probably *late Lower Devonian*', while Theron (1970) suggested the following ages based upon various invertebrate groups:

brachiopods—Emsian
asteroids—Lower Devonian–Lower Carboniferous
trilobites—Gedinnian (for the Gydo Formation).

BOLIVIA		ARGENTINA	BRAZIL		FALKLAND ISLANDS	SOUTH AFRICA
			Paraná	Amazonas		
Sicasica Formation	?					
	Cryphaeoides rostratus Zone	Chavela Formation				*Metacryphaeus venustus* Zone
	Cruz Loma Sandstone					Boplaas Formation
						Tra-Tra Formation
						Hexrivier Formation
Belén Formation	*Metacryphaeus tuberculatus* Zone		Ponta Grossa Shale	Ariramba Member		*Metacryphaeus caffer* Zone
	Metacryphaeus cornutus Zone					Gamka Formation
	Condoriquina Quartzite					
	Metacryphaeus giganteus Zone	Talacasto Formation			Fox Bay Formation	*Bainella africana* Zone
	Bainella insolita Zone					

Fig. 119. Suggested litho- and biostratigraphic correlations within the Malvinokaffric Realm.

On this basis Theron (1970: 201) was led to conclude that the Bokkeveld sequence was ' . . . clearly Devonian in age and probably mainly Lower Devonian'. Boucot & Johnson (*in* Hallam 1973) considered the brachiopod faunas of the Ceres Subgroup to indicate, *in toto*, an Emsian age.

The writer has pointed out elsewhere (Cooper 1977) the importance of eustatic sea-level changes to chronostratigraphic correlation and thus House's (1975) concise resumé of synchronous fluctuations in mean sea-level in the Old World Realm is of the utmost importance. There can be little doubt that these fluctuations (Fig. 120) are of eustatic origin and hence of global significance and, therefore, applicable to the Malvinokaffric Realm. There can also be no doubt that Bokkeveld sedimentation was initiated by marine transgression (Du Toit 1954), and that for an epicontinental sea to flood Gondwanaland to the extent of the Samfrau Sea there must have been a very significant relative rise in sea-level. It is of the highest significance, therefore, that widespread marine transgression was initiated only during the late Emsian in the period under discussion, and that this transgression peaked during the early Eifelian. In the writer's opinion, therefore, the Bokkeveld sequence cannot be older than late Emsian and the marine portion should be regarded as of late Emsian–Eifelian age. This is supported by the suggested correlation of the *Bainella africana* Zone with the Bolivian zone of *Metacryphaeus giganteus*, which was regarded by Wolfart & Voges (1968) as late Emsian in age. Moreover, as already noted, this is the level at which *Phacops (Viaphacops)*, typical of the late Emsian–Eifelian in the Old World Realm, enters the Malvinokaffric succession.

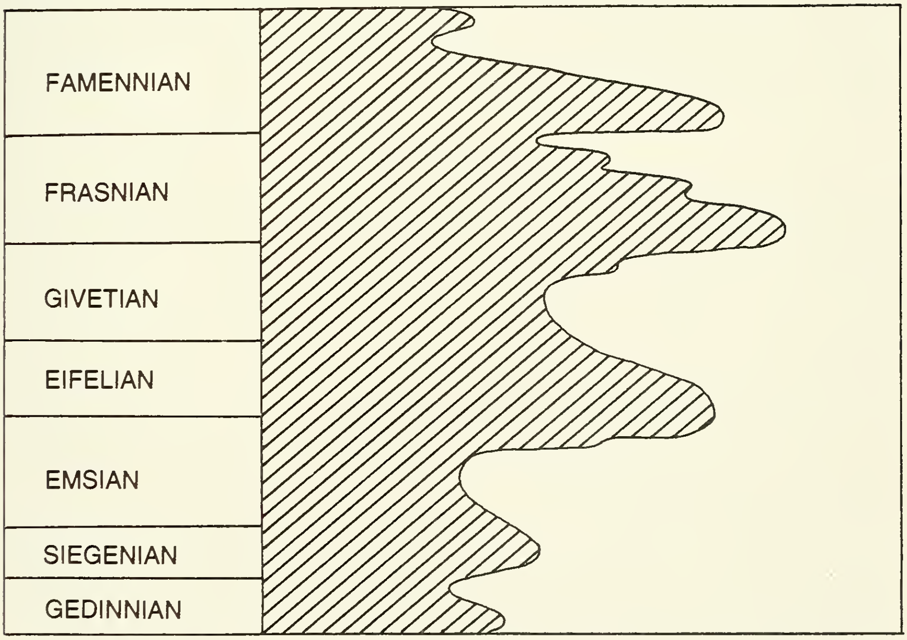

Fig. 120. Eustatic fluctuations in sea-level during the Devonian. (Data from House 1975.)

SUMMARY

The Bokkeveld trilobite fauna is revised and shown to comprise several distinct, stratigraphically separated faunal assemblages. The faunas from the Gydo Formation form the basis for the recognition of the *Bainella africana* Assemblage Zone and include the dechenellid *Ormistoniella malaca* (Lake), the dalmanitid *Francovichia clarkei* (Ulrich), the homalonotids *Burmeisteria herscheli* (Murchison) and *B. notica* (Clarke), together with the calmoniids *Bainella africana* (Salter), *B. arbuteus* (Lake), *B. cristagalli* (Woodward), *B. gamkaensis* (Rennie), *Kozlowskiaspis (Kozlowskiaspis) ceres* (Schwarz), *Typhloniscus baini* (Salter), *Pennaia pupillus* (Lake), *Phacopina* cf. *padilla* (Eldredge & Braniša), *Oosthuizenella ocellus* (Lake), *Renniella rossouwi* gen. et sp. nov., *Deltacephalaspis pseudoconvexus* (Reed), and *Metacryphaeus* sp. The *Metacryphaeus caffer* Assemblage Zone is represented by the faunas from the Voorstehoek Formation. These include abundant *Burmeisteria herscheli* (Murchison) and *Metacryphaeus caffer* (Salter), together with *Phacopina lakei* (Reed), *Gamonedaspis boehmi* (Knod), and rare examples of *Ormistoniella malaca* (Lake) and *Pennaia* sp. The Waboomberg Formation has yielded only *Metacryphaeus venustus* Wolfart and is thus accordingly designated the *Metacryphaeus venustus* Assemblage Zone. In addition to *Renniella*, two other new genera are proposed, *Ormistoniella* and *Oosthuizenella*, as well as the new subgenus *Metacryphaeus (Wolfartaspis)*. In addition, *Digonus* is considered a junior subjective synonym of *Burmeisteria* s.s. The suprageneric classification of the calmoniids is at present unsatisfactory and further work is required. Faunal affinities and evidence from eustatic changes in sea-level suggest a late Emsian age for the commencement of Bokkeveld sedimentation, with marine deposition continuing well into the Eifelian.

ACKNOWLEDGEMENTS

This project was commenced in 1973, while the writer was employed at the South African Museum, jointly with Dr B. F. Kensley, now of the Smithsonian Institution, Washington. As Dr Kensley was unable to complete this collaboration, I wish to express my thanks to him for assistance in the field, fruitful discussion on arthropod taxonomy, and for drawing a number of the reconstructions.

I am indebted to Mr R. Oosthuizen for making available much of the material discussed herein, for his thorough reading of the manuscript, and for his valuable advice derived from a detailed knowledge of the Bokkeveld trilobites, and to Mr R. Dick of the University of Cape Town who made available his private collection.

I should like to thank Mr W. Holleman of the Albany Museum for his assistance and for the loan of Schwarz's type material; Prof. P. Söhnge for access to material in the Geological Collections of the University of Stellenbosch; Dr C. L. Forbes of the Sedgewick Museum, Cambridge, for photographs, latex moulds and information on the Bokkeveld trilobites in his charge; Dr R. Fortey of the British Museum (Natural History) for photographs of, and access to, the material in his care; Dr J. N. Theron of the Geological Survey, Bellville, for access to material collected by him and advice on stratigraphy; and to Mr P. Beaumont for his efforts to locate the cephalon of *Dalmanites pseudoconvexus*. Mr J. van den Heever provided photographs of an example of *Kozlowskiaspis ceres* in the South African Museum collections. Dr A. Keyser of the Geological Survey, Pretoria, and Mr B. Newman of the Port Elizabeth Museum both gave assistance with the collections in their care, and their help is gratefully acknowledged.

I am grateful for the ready advice and guidance of Drs H. Alberti, A. J. Boucot, N. Eldredge, P. Lespérance, A. Ormiston, and R. Wolfart, and their efforts in supplying me with inaccessible literature. I am especially indebted to Dr N. Eldredge for his advice, constructive criticism of the manuscript, and for providing me with photographs of the holotype of *Oosthuizenella ocellus* (Lake).

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